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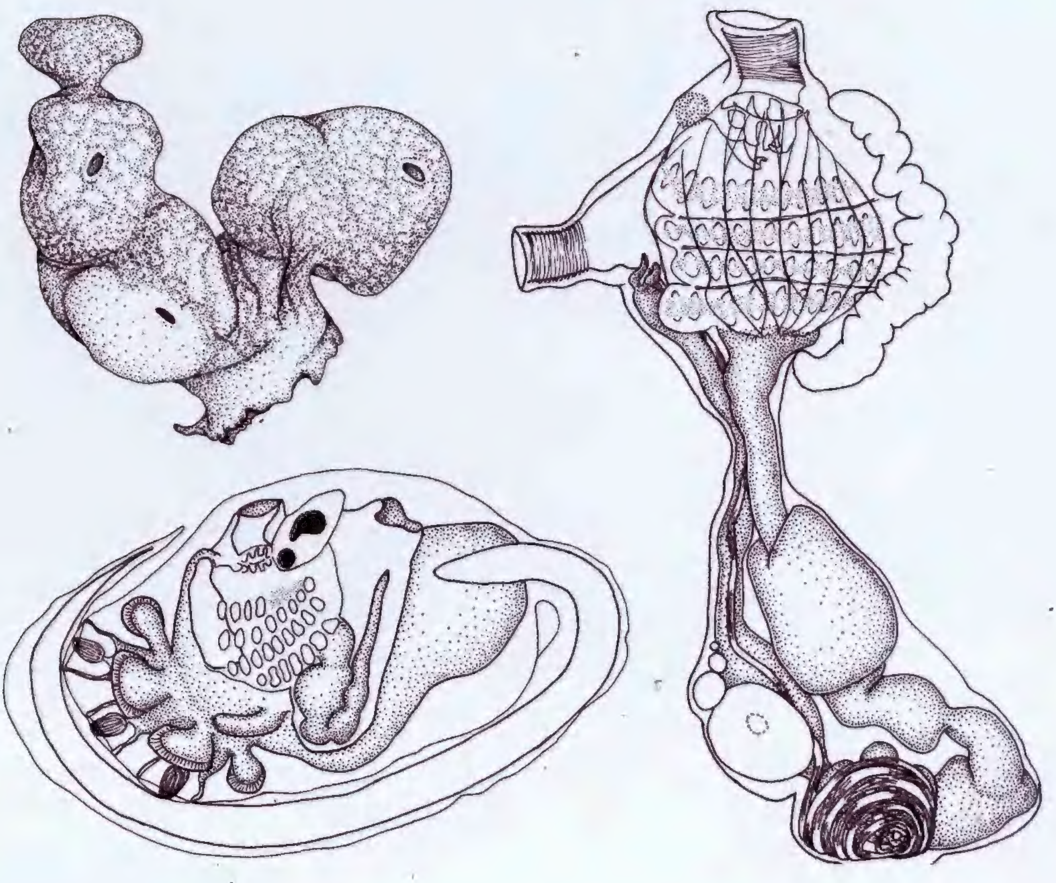


BRISBANE
15 AUGUST 2001

VOLUME 47
PART 1

THE AUSTRALIAN ASCIDIACEA
PART 4, APLOUSOBRANCHIA (3), DIDEMNIDAE

PATRICIA KOTT

Kott, P. 2001 08 15: The Australian Ascidiacea part 4, Aplousobranchia (3), Didemnidae. *Memoirs of the Queensland Museum* 47(1): 1-407. Brisbane. ISSN 0079-8835.

This fourth part of a monograph of Ascidiacea in Australian waters treats the Didemnidae which contains some of the smallest and most simplified zooids, and most extensive colonies and prolific replication rates known in the Class. The family is more speciose than others, largely as a result of diversity in Indo-West Pacific (including northern Australian) tropical waters where, despite a short free-swimming larval life, species have a wide geographic range. In Australia, indigenous species generally are found in the more temperate waters of the southern half of the continent. No evidence of pantropical range or of Atlantic species of Didemnidae exists in the western Pacific or eastern Indian Ocean. The affinities of the family with others in the Aplousobranchia are not clear, although a high vanadium content in *Leptoclinides* suggest an early origin from a *Diazona*-like ancestor. Intra-familial relationships are equally equivocal. Although there seems to be a trend to reduced zooid size from *Atriolum* and *Leptoclinides* to *Polysyncraton*, *Didemnum* and *Trididemnum*, similarities could be the result of convergence rather than evidence of phylogenetic affinity. *Clitella* gen. nov., *Lissoclinum* and *Diplosoma* have equally equivocal relationships with one another and with other genera. Of the 202 species described, 51 previously were known to occur in Australia, 35 were known only from other parts of the western Pacific and 116 are new. Colonial organisation, spicule size, form and distribution, and larval and zooid morphology of newly and previously recorded material have been scrutinised for taxonomic implications. Eight genera, *Atriolum*, *Leptoclinides*, *Polysyncraton*, *Didemnum*, *Trididemnum*, *Lissoclinum*, *Clitella* gen. nov. and *Diplosoma* are documented. In both tropical and temperate waters *Didemnum* is the most speciose genus in the family. Biological data on breeding seasons are indicated where possible. The new species include a number of previously unknown *Prochloron*/*Didemnum* symbioses. Crowded ectodermal columnar cells projecting from parts of the whole of the outer surface of adult zooids and pigmented squamous epithelium in certain species in a number of genera are reported although phylogenetic implications were not detected. Scanning electron micrographs of calcareous spicules are presented as an identification aid to complement the dichotomous keys to taxa. Species descriptions are complemented, where possible, with in situ photographs. An annotated glossary is included. The characters of species reported from adjacent areas (e.g. the western Indian Ocean, Indonesia, Malaysia and other western Pacific tropical locations to Fiji, as well as New Zealand), but not yet from Australian waters, are summarised and compared. ❐ *Indo-West Pacific, Prochloron symbioses, tropical, temperate, columnar epithelium, squamous epithelium.*

Patricia Kott, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 6 October 2000.

CONTENTS

INTRODUCTION

Species of the single family Didemnidae (Class Ascidiacea), one of 14 in the suborder Aplousoranchia, comprise a major component of the filter feeding communities in sublittoral locations, especially in tropical waters where their almost two-dimensional growth pattern and rapid rate of replication ensure that they occupy much of the available substrate. Their diversity in Australia far exceeds that in other parts of the world, possibly because of radiation of species from the western Pacific and their isolation around the southern parts of the continent where the majority of indigenous species occur. The

TABLE 1. List of Taxa — The formal page citations for new taxa erected in this work are indicated in this list, although a taxon may be informally referred to in preceding pages.

present work is the first comprehensive study of the family in Australian waters. Of the 202 species now recorded 116 are new and only 86 were previously known — 51 already recorded from Australia and 35 previously known only from other parts of the western Pacific.

The other Aplousobranch families are discussed in the Australian Ascidiacea parts 2 and 3 (Kott, 1990a;1992a) and part 1 (Kott, 1985) deals with the suborders Phlebobranchia and Stolidobranchia. Additional information including new species and records in the taxa treated in parts 1–3 of the Australian Ascidiacea are discussed in supplements (Kott, 1990b;1992b). About 600 species of Ascidiacea are now known to occur in Australian waters. Much material in all suborders, including the Didemnidae remains to be examined.

All specimens referred to by a museum registration number were examined in the course of this study. Where a sample of a colony or specimen lot is lodged in a second institution its registration number is given in italics following the registration of the principal lot.

Museums holding ascidian material examined during this study, with their abbreviations, are: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York, U.S.A.; BMNH, Natural History Museum, London, UK; MV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; TM, Tasmanian Museum, Hobart; WAM, Western Australian Museum, Perth; USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C. USA; SM, Senckenberg Museum, Frankfurt, Germany; ZMA, Zoological Museum of Amsterdam, University of Amsterdam, The Netherlands; ZMC, Zoological Museum, University of Copenhagen, Denmark; ZMH, Zoological Museum, University of Hamburg, Germany. Photographic collections relating to this material include the Australian Marine Photographic Index (AMPI, Neville Coleman); South Australian Museum (with prefix PE, K. Gowlett Holmes and others); and the Queensland Museum.

Throughout this work a senior synonym is preceded by '<' and a junior synonym by '>'.

Zooids have relatively few reliable morphological characters owing to their small size and overall uniformity — a result of simplification and convergence. Further, contraction often obscures significant zooid characters, the form of colonial systems often are difficult to determine, colony shape and size are affected by age, environmental factors and preservation and colours are variable and affected by oxidation and preservative. These factors have been a major constraint to accurate species definitions and determinations, which both depend to a great extent, on larval characters and spicule size and form. As in all colonial ascidians, larvae are viviparous, and in most taxa have been found being brooded in one or more colonies. The month in which they occur has been recorded.

TABLE 2. Measures of spicule ray length.

General description of rays	Very long	Long	Moderate	Short	Very short
Ray length relative to central spicule mass diameter	≥ 3	≥ 2	~ 1	≤ 0.5	≤ 0.2
Ratio of ray length to spicule diameter	3/7 = 0.43	2/5 = 0.4	1/3 = 0.33	0.5/2 = 0.25	0.2/1.4 = 0.14

Spicules have traditionally been defined by their size (maximum diameter) — the distance between the points of rays on opposite sides of the sphere, and by the number of rays in optical transverse section. Each species has spicules of a characteristic size range. Spicules of maximum diameter occur relatively frequently (mixed with others of lesser diameter) and are readily detected (by light or scanning electron microscopy) in preparations of strips of test from 5mm long. The maximum spicule diameter is used to define species in the keys and descriptions that follow. The significance of average or mean values for spicule size is doubtful without an accurate assessment of standard deviations, an indication of the full range of sizes and some measure of the variations in frequency of different sized spicules. Interpretation of spicule form by light microscopy has been subjective and is not always reliable. Scanning electron microscopy has allowed more critical interpretations of these 3-dimensional, opaque structures. A more or less pentagonal arrangement of each whorl of spicule rays has been demonstrated, making possible relatively accurate counts of the numbers of rays in a so-called optical transverse section. Also

used in the present work to describe the spicules and their rays is an assessment of the ray length/spicule diameter ratio (Table 2). In the spicule atlas (Figs 157–178) similar spicules are grouped (rather than arranged in species alphabetical order) for ease of comparison.

There have been few studies on the Ascidiacea in Australian waters and, probably because of the problems set out above, even fewer on the Didemnidae. Previous attempts to study the family often were unsuccessful because characters for species determination had not been identified, and in many cases similarities in the small simplified, convergent and often contracted zooids distracted attention from other characters, frustrated attempts to separate species from one another and resulted in many wrong assignations. Revision of much of the Pacific material in the Zoologische Museum (Amsterdam) and the US National Museum (Washington D.C.) has shown that Sluiter (1909), Van Name (1918) and Tokioka (1967) had similar problems in defining species parameters. Nevertheless, these works and the associated well conserved collections are the basis for more recent studies on the didemnid fauna of the tropical western Pacific. Few other authors had reported on any significant collections of didemnids in the tropical western Pacific until the past decade. The exceptions are Eldredge (1967) on the Didemnidae of the central Pacific; Tokioka (1950, 1952, 1955, 1961, 1967, 1970) and Millar (1975) on collections containing some Didemnidae from the central to western Pacific; and Kott (1977, 1980, 1981, 1982a) on didemnids in symbiotic relationships with prokaryotic chlorophyll-containing algae which, associated with an emerging world interest in this symbiosis, were the first systematic works on large collections of exclusively didemnid ascidians from the tropical western Pacific. The species list of Didemnidae in this part of the world has increased as a result of work in New Caledonia (Monniot, 1989, 1991, 1992, 1993, 1994, 1995), French Polynesia (Monniot & Monniot, 1987) and other locations (Monniot & Monniot, 1996; Nishikawa, 1984, 1994).

Monniot (1993) was surprised that none of the 8 species of *Polysyncraton* recorded from New Caledonia were known from other locations in the SW Pacific. She suggests this is because the collections were made by SCUBA rather than dredge or shore collecting (although this would surely have affected other genera as well as *Polysyncraton*). It has been found in the present study that colonies in the intertidal rubble zone are not as large as some found subtidally, but there is no evidence that SCUBA diving is sampling a different fauna from that sampled by shore collecting at low tide. The large number of new species taken from New Caledonia and those described herein apparently reflect our ignorance of the didemnid fauna. It is not evidence of either isolation, or habitat specialisation. Most of the tropical species in this family are now known to have a wide geographic range.

These studies have established some appreciation of the intraspecific variation that can be expected to occur amongst populations over wide geographic ranges in the Indo-West Pacific. Proposals of pantropical species ranges resulting from transport on ship's hulls (Rocha & Monniot, 1993) or any other cause are speculative and the conspecificities on which these proposals are based are not confirmed by the present study.

In temperate waters the didemnids of the *Challenger* expedition (Herdman, 1886), provide the basis for study of the family. Reports on small collections from south-western Australia (Michaelsen, 1930), New South Wales (Herdman, 1899; Kott, 1972c), southern Australia (Kott, 1972a-b, 1975, 1976) and other general collections (Kott, 1962) did not appreciably advance understanding of Didemnidae in these waters owing to the same lack of understanding of the group that beset studies in other parts of the world.

Few species of the Didemnidae have a continuous range from tropical into temperate waters, such a range occuring more often in other families of Ascidiacea (see Kott, 1985, 1990a, 1992). As with other taxa, more indigenous species occur in temperate than tropical waters, although Didemnidae are more diverse in tropical waters (Kott, 1982c), reducing diversity toward the poles. Two tropical species known from Australian waters may possibly occur in New Zealand, viz. *Polysyncraton fuscum* (?*P. meandratum*) and *P. paradoxum* (?*P. robustum*). However, although possible Gondwana ascidian relicts have been recorded from Australian and New Zealand temperate locations, there are no records of didemnid species in this category (see *Didemnum fragum*).

Kott (1998) documented 59 valid species previously recorded from Australia. *Didemnum incanum,* removed from synonymy and validated in the present work, should be added to the total.

Of these 60 species, *D. rottnesti* Kott, 1962, *Polysyncraton victoriensis* Kott, 1976 and *D. fimbriatum* Herdman, 1899 await revision and their status is uncertain. A further 6 species said to occur here result from misidentification, viz *Didemnum augusti*: Kott, 1962, *D. lambitum*: Kott, 1962; *Polysyncraton mortenseni*: Kott, 1954; *Trididemnum cerebriforme*: Kott, 1962 and *T. spiculatum* Kott, 1962.

ACKNOWLEDGEMENTS

During this study, I have had the support of colleagues both in Australia and overseas. In particular, I thank the successive Directors and Boards of the Queensland Museum for their continued support. I also thank Curators and Collection Managers in Australian and overseas museums for their very prompt responses to my requests for loan of specimens — in Australia Penny Berents (Australian Museum), Sue Boyd (Museum of Victoria), Loisette Marsh and Jane Fromont (Western Australian Museum) and Wolfgang Zeidler, Karen Gowlett Holmes and Thierry Laperousaz (South Australian Museum); and from overseas Joke Bleeker (Zoological Museum, Amsterdam), Sheila Halsey (the Natural History Museum, London), Hilke Ruhberg (the Zoological Museum, Hamburg) and Linda Cole (the US National Museum of Natural History, Washington D.C).

I have been fortunate in the richness of the collections available to me and the comprehensive sampling of the Australian coast they represent. Much of this collecting has been by SCUBA diving, yielding mature, undamaged colonies. The Western Australian Museum (especially Shirley Slacksmith and Loisette Marsh) took material, by dredge as well as SCUBA, from all the western Australian coast including the North West Shelf. Jan Watson has extensively sampled the Victorian coast. The South Australian Museum (especially Wolfgang Zeidler, Karen Gowlett Holmes, Hugh Bavenden) and South Australian Fisheries Department (Scoresby Shepherd and his team) have sampled the Gulf St Vincent, Spencer Gulf and the Great Australian Bight. Karen Gowlett Holmes photographed samples from across the southern coast from Tasmania to Albany and from the Northern Territory. I have also had available the collection (now in the Queensland Museum) made by the Australian Institute of Marine Science (AIMS) Bioactivity Group from all around the continent, including the Kimberley coast, the Arafura Sea and the Great Barrier Reef (McCauley et al., 1993).

I am grateful to the photographers who have made it possible for me to appreciate the living appearance of many of the species — especially Neville Coleman (Australian Marine Photographic Index), Karen Gowlett Holmes (South Australian Museum), Roger Steene (Cairns), Ron and Valerie Taylor (Sydney), Myriam Preker (Heron I. Research Station) and members of the AIMS Bioactivity Group.

I acknowledge with particular gratitude the work of my successive research assistants both in the laboratory and in the field, John Kennedy (1991–3), Susan List (1994–6) and Daniel Schmidt (1998–2000). John Kennedy drew many of the black and white figures of *Leptoclinides* and *Atriolum* and produced the scanning electron micrographs of their spicules. Susan List and Daniel Schmidt drew the remainder of the figures and prepared and scanned spicules of more than 1000 specimens of *Didemnum*, *Polysyncraton*, *Trididemnum* and *Lissoclinum*. As well as drawing many of the figures, Daniel has revised and updated most of the others and has composed the paste ups and scanned these and the colour plates. In executing these responsibilities he has demonstrated an appreciation of the Didemnidae that has significantly advanced this work.

Also, since 1980, able and enthusiastic assistance in the field has been provided, at various times, by Andrew Rozenfelds, Lucille Crevola-Gillespie, Stephen Cook, David Parry and Myriam Preker. Georgia Pass generously helped with the initial pasteups of many of the figures. Jennifer Mahoney, Audra Topping, Lynette Dickfos, Katie Laws and Jennifer Cannon successively updated the manuscript as it developed through its many drafts, and I thank them for their co-operation, diligence and good humour. I also thank Mr U. Tinggi of the Scientific Service in the Queensland Health Department, for his analysis of a sample of *Atriolum robustum* for vanadium.

I am grateful to my colleague, Dr Lester Cannon, for sharing his wide knowledge of taxonomy and invertebrate structure and function with me over the past 20 years.

Since 1980, grants from various agencies have supported the field and laboratory programme as collections were made and examined, data compiled and manuscripts prepared for this Monograph. The agencies are the Australian Biological Resources Study 1980–2; Marine

Sciences and Technology Grants Scheme 1984–86 and the Australian Research Council 1991–3, 1994–6 and 1998–2000.

PROCEDURES

Formalin fixed, and preferably narcotised specimens are essential to adequately dissect and observe the morphology of specimens of the Ascidiacea. This is particularly true for Didemnidae, which have especially small zooids in complex systems. Long term preservation specimens should be transferred to 70% ethanol after at least 2-3 months in fixative. In all genera of this family, following observations on surface structures, a thin vertical inspection slice or wedge, through the whole depth of the colony from a common cloacal aperture to the outer margin, will display the general form of the cloacal systems, the position of the zooids, and the distribution of bladder cells, spicules and other inclusions in the test. The inspection slice is always cut parallel to the long axis of the zooids — i.e. generally at right angles to the upper surface and thick enough to include whole zooids but thin enough for light microscopy. Efforts should be made not to excessively mutilate the colony. Neither didemnid nor any other ascidian colony should ever be cut horizontally (parallel to the surface), for this divides the zooids and obscures the configuration of the cloacal cavities.

Zooids and embryos can be observed in situ in these inspection slices, or they can be removed for manipulation and dissection. Care needs to be taken to avoid tearing off branchial or atrial siphons when removing zooids. It usually is not possible to remove didemnid zooids entire. They invariably break across the oesophageal neck. Zooids can be dissected with sharpened needles or forceps in a drop of glycerol on a glass slide. Sometimes a drop of stain added either to the colony itself or to the slice of it, or to the zooids and embryos (after their removal) will help to display their structure. Often zooids are held so tightly in the test that they cannot be removed and it is necessary to decalcify the hand-cut section of colony in order to observe the zooid structure. Hand-cut thin sections of colony can be decalcified by dropping into an excavated block or watch glass with sufficient 3% HCl to cover the section. Generally decalcification will be completed in 1–3 hours, although often it is necessary to renew the acid owing to the buffering effect of the calcareous spicules.

Leptoclinides and *Atriolum* have large zooids in which organs can be readily observed by dissection and manipulation, although they are not always easy to remove from the colony and are best observed in situ. In other genera the structure of small zooids can be adequately examined only in stained and cleared permanent mounts of either the isolated zooids or the hand-cut, thin, decalcified sections of the colony. Larvae also are stained and mounted for light microscopy.

Spicules are prepared for SEM by incinerating a small fragment of test (to remove all organic material) on the tip of fine forceps. They are then put into a drop of absolute alcohol on the top of an adhesive surface on the stub. The spicules separate from one another in the alcohol and settle fairly evenly before the alcohol evaporates, leaving a suitably clean surface for coating. In order to avoid 'drowning' the spicules, it is essential that the adhesive used does not dissolve in the alcohol — in the present study Avery 'Spot-O-Glue' tabs were used.

In addition to the general subjective accounts of colour, many living specimens were compared (in the field) with colour charts (Ridgway 1866) to give a more precise and objective account of colour and these are indicated in the text by a superscript R (e.g., rose red ^{R})

Permanent slide mounts of most zooids and larvae for light microscopy, as well as photomicrographs and scanning electron microscopy stubs of spicules are in the Queensland Museum collection.

Analysis for vanadium content of a freeze dried sample of *Atriolum robustum* was by nitric peroxide wet digestion followed by determination with ICP-AES.

Family DIDEMNIDAE Giard, 1872

The family is relatively uniform although very speciose. It is characterised by its small zooids divided into thorax and abdomen, the former consisting of a large pharynx perforated by 3 or 4 rows of stigmata. Gonads, in the abdomen respectively dorsal or posterior to the short, vertical or ventrally flexed gut loop, consist of a small ovary with only one egg maturing at a time, and dome-shaped to spherical or oval testis, entire or subdivided, with the vas deferens either straight, or coiled around the testis. The zooids are arranged in usually extensive cloacal systems. With the exception of *Diplosoma* and a few species in each of the other genera except *Leptoclinides* and *Atriolum*, the test contains minute (seldom more than 0.1mm diameter and

often less than half that size), stellate, globular or burr-like, calcium carbonate (aragonite) spicules synthesised in paired lateral organs in the parietal thoracic wall. Body wall musculature is confined to the thorax, and never occurs in the abdominal wall. Usually (except in *Atriolum* and *Leptoclinides* and a few species in other genera) a retractor muscle projects out into the test from the ventral surface of the oesophageal neck of the zooid and 2 or 3 vascular projections, each with a terminal expansion (ampulla) extend into the test from the ventral side of the pole of the gut loop.

The Didemnidae have long been regarded as the most highly evolved of aplousobranch ascidians. Certainly colony organisation, and zooid size-reduction and simplification, are more advanced in this family than in others. It is possible also that integration of the colony is well advanced, a nerve complex having been demonstrated (Mackie & Singla, 1987). Nevertheless, these developments of colony and zooid do not imply direct linear evolution through the Aplousobranchia. Compelling evidence of an early origin for the Didemnidae exists in the presence, in *Leptoclinides*, of very large amounts of vanadium generally found in more primitive ascidians such as *Ciona* (Hawkins et al., 1983). Unless the Didemnidae is polyphyletic, which seems unlikely, these high concentrations of vanadium suggest that *Leptoclinides* is the more primitive genus, and that the evolution of other genera has been associated with loss of atrial siphons, reduction in zooid size and loss of vanadium. The related genus *Atriolum* has larger zooids than *Leptoclinides* and, like a few *Leptoclinides* spp., has a functional oviduct — the ovum passing from the abdomen through the oviduct to a thoracic brood pouch where it is incubated. Thus, some characters of *Atriolum* are more primitive than in other Didemnidae. However, *Atriolum* has an undivided testis (like *Didemnum*). Further, although *Atriolum* has been found to contain vanadium it is in lower concentrations (350ppm in *A. robustum*) than in *Leptoclinides* spp. (Hawkins et al., 1983: 8,000–10,000ppm) which may indicate a *Leptoclinides* ancestor

There are few morphological clues to phylogeny in the Didemnidae largely because of size reduction and simplification which have resulted in a preponderance of convergent characters of doubtful relevance to phylogeny. There is an apparently significant progressive reduction in zooid size from *Atriolum* to *Leptoclinides* to *Trididemnum* (which often retains the *Leptoclinides*-like atrial siphon) to *Didemnum*. *Polysyncraton* zooids are not so small, and they have *Leptoclinides*-like multiplicity of male follicles, relatively numerous stigmata and a coiled vas deferens. Condition of the testes and of the vas deferens may be indicative of generic relationships, viz. a coiled vas deferens is present in *Leptoclinides* and *Polysyncraton* (with many ♂ follicles), and *Atriolum*, *Trididemnum* and *Didemnum* (each with an undivided testis). The straight vas deferens of *Lissoclinum*, *Clitella* and *Diplosoma* may indicate another group of related species. The retractor muscle (probably associated with reduction in length of the thorax and loss of muscles from the abdomen) in 6 of the 8 genera (all except *Atriolum* and *Leptoclinides*) does not necessarily indicate a common origin .

Romanov (1989) proposed that a straight vas deferens and absence of spicules are primitive features and therefore *Diplosoma* and related *Lissoclinum* are primitive. However, there is no evidence to support a primitive status for these characters. *Diplosoma* (the only genus consistently lacking spicules) has complex larvae with precocious blastozooids forming in the trunk and contains species with prolific replication in which primary, secondary and even tertiary buds form before separation from one another. Although in Cionidae and Diazonidae regeneration of the thorax on a conserved abdomen probably is an early stage in the evolution of replication in the Aplousobranchia (Kott, 1990a), a similar process observed in *Diplosoma* by Romanov (1989) is more likely convergent than primitive.

Larfargue (1983) proposed the linear evolution of didemnid genera from *Cystodytes* (Polycitoridae), through *Lissoclinum* to *Polysyncraton* and *Didemnum* to *Trididemnum*, while *Diplosoma* is derived from *Lissoclinum* by loss of spicules. Larfargue (1983) has not included *Leptoclinides* in her considerations, being primarily concerned with Didemnidae from the French coast. The present study suggests that a linear relationship of the genera is unlikely, and that derivation of the family (with the Diazonidae or Holozoidae) from some common ancestor is more likely than from the Polycitoridae (see discussion on *Atriolum*, below).

Didemnid genera are distinguished from one another by the presence or absence of spicules, condition of the testis (undivided or bisected, or divided into more than 2 follicles), course (and

length) of the vas deferens (hooked proximally but otherwise straight, vertical, and relatively short; or a longer duct, its length taken up in its spiral course around the testis), presence or absence of a retractor muscle, presence or absence of an atrial siphon, and number of rows of stigmata (3 or 4). Species are distinguished from one another by zooid size (generally directly related to the number of stigmata per row), presence or absence of an anterior atrial lip (or tongue), orientation and general proportions of the gut, numbers of coils of the vas deferens, size, shape and distribution of the spicules, form of the colony and common cloacal systems and size and form of larvae. Position, shape and size of the lateral organ are affected by contraction of the thorax and are generally significant characters for species determination only within limits.

ANNOTATED GLOSSARY

The following entries relate specifically to the Didemnidae. They should be used in conjunction with glossaries on aspects of all families of the Ascidiacea (Kott, 1985, 1990a, 1992a).

atrial apertures, — siphons: Atrial apertures are on long muscular siphons in *Leptoclinides*, *Atriolum* and usually in *Trididemnum*. In other genera (excepting *Didemnum fucatum* which has a small circular sessile opening) the atrial aperture is a large sessile opening that exposes a large part of the perforated branchial sac directly to the cloacal cavity. In certain *Didemnum*, occasionally in *Lissoclinum* and commonly in *Polysyncraton*, an anterior tongue (sometimes called a lip) projects from the anterior rim of the opening. It is muscular, and in many species in which it occurs its length is related to the position of the zooid relative to the common cloacal aperture. The tip of the atrial tongue (especially in *Polysyncraton*) often is bifid and sometimes has a fringe of small papillae along its edge. It can be inserted into the test over the common cloacal cavity or it may be expanded and increase in length to extend through the roof of the common cloacal cavity into the rim of the common cloacal aperture. The zooid then has some capacity to control water pressure in the colony and in the pharynx either by closing the common cloacal aperture or by pulling the roof of the common cloacal cavity down over the common cloacal canals and over the atrial apertures.

atrial lip, — tongue: see **atrial aperture**.

blastozooids: see **larvae, replication**.

branchial apertures, — siphons: Branchial apertures always are on cylindrical siphons which sometimes, especially in *Didemnum*, are particularly long. The siphons are relatively uniform, with 6, usually pointed projections or lobes around the rim of the apertures, although in some *Leptoclinides* the pointed lobes around the aperture are not developed. The test always projects to line the siphons, very often, with spicules which either form a plug in the siphon or appear (from the surface) to line the margin of a stellate opening. The shape of the openings appears to be determined by a stellate cross section of the lumen of the siphon, possibly caused by longitudinal muscles inserted into the branchial lobes.

branchial sac: see **stigmata**.

colony shape: Convergence in the form of colonies is conspicuous, most genera containing representatives of the full range of shapes from small one-system cushions with a central common cloacal aperture to more extensive single or multi-system colonies. The thin sheet-like irregular colonies, containing randomly distributed common cloacal apertures are probably the most commonly encountered colony form in most genera except *Atriolum* and *Leptoclinides* which tend to form more 3-dimensional shapes with terminal common cloacal apertures on elevated parts of lobed or irregular fleshy masses. Some species in most genera except the soft *Diplosoma* and *Lissoclinum* have finite and characteristic shapes, e.g. flask-shaped, spherical, stalked or small oval or circular cushions. Upright colonies or projecting lobes sometimes are supported by the basal test expanded up into a pillar or solid central mass, partially separated from the surface zooid-bearing layer of test by a cloacal cavity; or water pressure in a large central cloacal cavity maintains the shape of the colony. Some massive 3-dimensional colonies in *Leptoclinides*, *Didemnum* and often *Trididemnum* are branched or fold over and the surfaces coalesce to form 3-dimensional reticular or sponge-like structures with external surfaces and spaces as well as extensive common cloacal spaces enclosed in the colony (*Leptoclinides echinus, Didemnum clavum, D. complexum, D. ossium, D. lissoclinum, D. psammatode, D. spongioide, Trididemnum crystallinum, T. lapidosum, T. nobile, T. sibogae* and *T. vermiforme)*. Many species *(e.g. Lissoclinum bistratum, Didemnum molle, Diplosoma virens*) lobulate and the replicates move apart, spacing themselves evenly

over the substrate (Ryland, 1990). Extensively branched tree-like structures (e.g. *Didemnum ossium*, *D. lissoclinum*, *Trididemnum lapidosum*) often have a hard core of packed spicules which serves as a supporting frame through the centre of each branch (see also **cloacal systems**; **common cloacal apertures**; **colony surface**; **substrates**).

colony surface: The colony surface is either smooth or (less often) has surface ridges (see *Didemnum spongioide*) or papillae. Some species have small spicule-filled papillae on the whole or part of the surface which make it rough or raspy. A few species in *Didemnum* (e.g. *D. cuculliferum)* and occasionally *Polysyncraton* (*P. echinatum*) have a hollow spiky papilla associated with each branchial aperture which accommodates an enlarged ventral lobe of the branchial aperture. These papillae appear to protect the branchial apertures (*Didemnum cuculliferum*). The surface may also be raspy if spicules are crowded and/or large in the superficial layer of test, although they are not always present there, the superficial layer of test being crowded with spherical bladder cells (often mixed with pigment cells) which can create a particularly smooth surface. Many colonies, especially when preserved, have the surface marked by a mosaic of circular to oblong areas separated from one another by narrow depressions. These depressions, usually lined on each side by zooid openings, are formed by the collapse of the thin layer of test forming the roof of the primary common cloacal canals that surround solid stands of test or clumps of zooids.

colour: Colours derive from pigment cells in the test, blood cells (which often diffuse into the test and symbionts in the test) or in the common cloacal cavity. All colour appears to change, probably as a result of oxidation following collection and fixation, and generally is an unreliable character for identification. A black pigment spot — endostylar pigment cap — on the anterior end of the endostyle occurs in the *cyclops* group of *Trididemnum* species and others in.the same genus. Similar spots are in the mid-dorsal line near the neural ganglion in *Diplosoma* spp. (see also **squamous epithelium**.)

common cloacal apertures: Common cloacal apertures usually are raised above the surface of a colony where the excurrent water flow is entrained by passing currents, thus keeping it separated from the smaller incurrent streams entering each branchial aperture (see Kott, 1989). Elevated common cloacal apertures are either on chimney like projections of the test, or they are

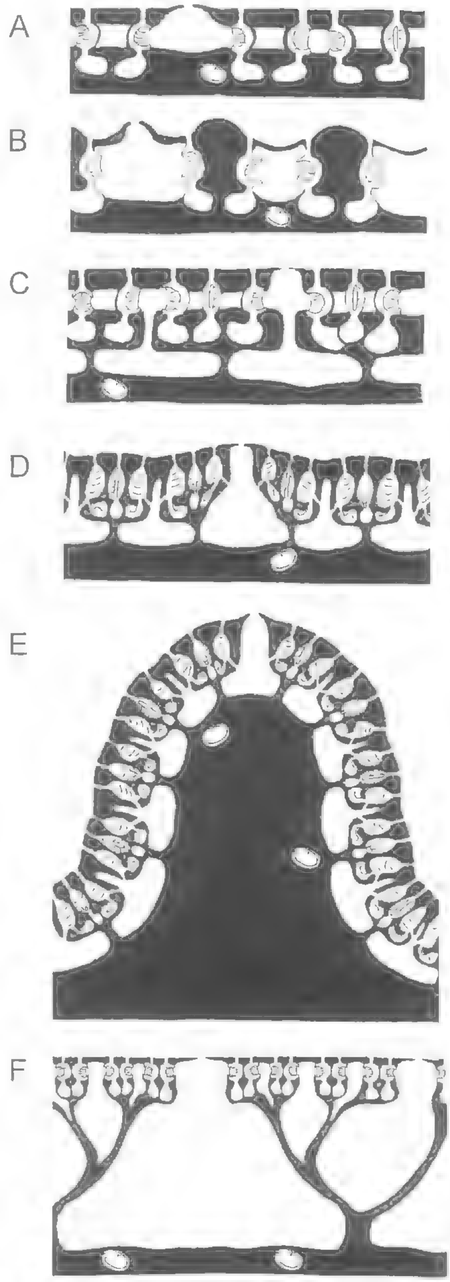


FIG. 1. Common cloacal systems (diagrammatic). A, horizontal thoracic cavity; B, thoracic primary canals lined with zooids; C, deep primary canals and secondary thoracic and posterior abdominal cavities; D, sheet or cushion-like colonies with sessile common cloacal apertures and atrial siphons opening into posterior abdominal cavities (cf. *Leptoclinides*, *Trididemum* spp.); E, cones or lobes with central test core and terminal common cloacal apertures. F, clumps of zooids in terminal branches of test connectives (cf. *Diplosoma* spp.).

terminal on elevated parts of the colony — on upright colonies or on vertical lobes or swellings caused by structural thickenings of the basal test to form an axial core of test which support the upright colony or elevations or colony lobes. Elevations also are created by pressure of the excurrent water which inflate the surface over the large common cloacal chambers (beneath the cloacal apertures). In some colonies, however, sessile common cloacal apertures are not conspicuously elevated and there is no obvious separation of incurrent and excurrent water currents except the differences in their relative strength (Kott, 1989; *Polysyncraton echinatum*).

common cloacal cavities: Common cloacal canals or horizontal spaces are either shallow, at thoracic and/or oesophageal level; or they are deeper, extending the length of, and sometimes into posterior abdominal cavities behind, the zooids. The small zooids are embedded in test around or above cloacal canals and spaces; or the cloacal spaces penetrate the test surrounding the the zooids or penetrate into clumps of zooids separating them from one another so that (depending on the depth of the cloacal cavity) some part or the whole of their thorax, supported by a narrow ventral strip of test, is completely surrounded by cloacal space, the thoraces stretching between the surface and a thicker basal layer of test in which abdomina are embedded. Especially in *Lissoclinum* and *Diplosoma*, whole zooids or clumps of zooids stretch between the surface and basal layers of test with the abdomina embedded separately or in clumps in the test strand (Fig. 1).

dispersal: see **gene flow**.

ectodermal ampullae: see **larvae**.

endostylar pigment cap: see **colour**.

epidermis: see **projecting columnar cells, squamous epithelium**.

fertilisation: Fertilisation is internal, the egg generally is fertilised in the abdomen of the zooids, through the vestigial oviduct (Burighel et al., 1986; Martinucci et al., 1988, Ryland & Bishop, 1990, 1993; Bishop & Ryland, 1991; Burighel & Martinucii, 1994a,b). The embryo passes into the test directly from the abdomen, is incubated in the test, and liberated as a free-swimming larva either through the common cloacal cavity, or directly through the surface test. Only in *Atriolum* Kott, 1983 and some *Leptoclinides* (e.g. *L. brandi*) does the ovum move up the oviduct into a thoracic pouch where it is fertilised and incubated. Very occasionally the embryo remains in an abdominal pouch attached to the abdomen of the zooid (*Diplosoma ferrugeum*).

gene flow: Although some apparently indigenous species have restricted ranges, many species of the Didemnidae in tropical as well as in temperate and polar waters, have a wide geographic range despite being internally fertilised and brooding their larvae. In those species with known life histories, the free-swimming larval life is less than 20 mins (Olson, 1983) and occasionally larvae appear to begin their metamorphosis before liberation from the parent colony (*L. durus*). In such cases, larval dispersal over great distances seems unlikely and gene flow probably occurs through chains of recruitment between adjacent locations. Nevertheless, larval free-swimming life may be extended when stimuli to settle are not available (e.g. open sea without shadowed undersurfaces — Berrill, 1955, or night-time — Olson, 1983), providing opportunities for alternative strategies — one for gene flow, and one for population maintenance (Kott, 1980, 1985). Another possible agent for gene flow between populations of widespread species, separated from one another by vast expanses of deep ocean (such as Fiji and other parts of the western Pacific, and Hawaii), may be transport by driftwood, the slow recruitment rate likely to be associated with such transport possibly being accommodated by longevity of the colonies (Jackson, 1986).

geographic range: see **gene flow**.

gut, gut loop: The vertical oesophageal tube, smooth and almost spherical stomach, and thick cylindrical duodenum (often expanded distally) form the descending limb of the gut loop. A posterior stomach is in the pole of the loop, and the rectum forms the ascending loop. Usually these divisions are separated from one another by constrictions, and there are no short lengths of mid-intestine between them as in other aplousobranchs (Kott, 1990a,b). The oesophagus and stomach are always to the right of the rectum. The posterior stomach is more or less oval in most genera, although in *Polysyncraton* it is a roomy organ which expands to join the rectum. The rectum may form an elbow where the posterior stomach joins it. The proximal part of the rectum is wide and in most genera is separated from a narrower upper distal part by a short length of narrow gut surrounded by tubules of the gastro-intestinal gland. In *Polysyncraton* the distal part of the rectum is a particularly narrow cylindrical tube. Separation of the proximal from

distal rectum is abrupt in *Lissoclinum*. In *Clitella* a prerectal chamber is constricted off from the distal rectum. The post-pyloric part of the gut loop is sometimes short, straight and vertical; or longer and flexed ventrally sometimes being more or less at right angles to the oesophagus and the long axis of the zooid. The distal (post-pyloric) part of the gut loop may be bent up against the proximal part (e.g. in *Leptoclinides dubius* and related species) forming a double loop. The anal border is always divided into 2 lips.

haemocoel: Possible products of the haemocoel are large brown spherical cells (0.008–0.01mm diameter) observed in the larval and adult haemocoel in *Didemnum parancium*, *D. verdantum* and *D. viride* and (except in *D. parancium*) free in the test (sometimes surrounding the adult zooid). In *D. fuscum* and *D. sordidum* similar cells are in the larval haemocoel and are conspicuous around the outside of the zooids. In *D. spadix* and *D. etiolum* they have been found free in the test around the zooids but have not been observed either in the larval or adult haemocoel. Similar cells are also in the adult haemocoel of *Lissoclinum badium*, *L. conchylium*, *L. durabile* and *L. reginum* and in the test around the zooids in *L. caliginosum* and *L. ostrearium* — all species of the *fragile* group of *Lissoclinum*.

larvae: Larvae are diverse. Differences occur in the accessory adhesive apparatus at the anterior end of the trunk, presence and number of blastozooids, position of the oozooid and blastozooids (if any) in the trunk, length of the tail and size of the trunk. The larval test, especially in *Lissoclinum* often contains inclusions of unknown affinity that appear not to be blood or test cells, or spicules. The outer cuticle of the larval test may be marked with fine striations and ornaments (Cloney, 1990). In species with obligate symbioses with plant cells, the test of the larval trunk is modified to entangle the symbiotic cells and carry them to the new generation colonies (Kott, 1982b; below). Generally the larval trunk is deep with a large yolk mass, and a vertical pharynx and gut loop. An otolith and ocellus are invariably present in the cerebral vesicle. Usually three stalked adhesive organs are in the anterior mid-line. Each has a deep axillary cone in an equally deep epidermal cup — superficially like the adhesive organs of *Distaplia* (Cloney, 1977). Very occasionally, apparently associated with swiftly flowing currents (Kott, 1980), there is a dramatic increase in the number of adhesive organs (e.g. 30 in *Diplosoma multipapillatum* Kott, 1980, 15–20 in *Polysyncraton multipapillae* Monniot, 1993, and 5–9 in *Lissoclinum badium* Monniot & Monniot, 1996). Only in *Clitella* which has 2 convoluted adhesive ridges in continuous grooves instead of 3 stalked conical adhesive cones in an epidermal cup is there a significant difference in the adhesive organs. There are only 2 adhesive organs in *Trididemnum cyclops*, *Didemnum albopunctatum*, *D. parancium*, *D. poecilomorpha*, and *D. pitipiri* Monniot & Monniot, 1987.

Usually 4 conical to finger-like epidermal ampullae are along each side of the median line, although sometimes (usually in *Polysyncraton* and in some *Trididemnum* and *Didemnum*) they are more numerous (up to 24 or more). Enlarged epidermal cells often form a terminal cap on each ampulla. Ectodermal ampullae are fewer in most species of *Diplosoma*. In *Diplosoma* the oozooid and blastozooids tend to be in the anterior part of the trunk associated with the adhesive array rather than in the centre of the trunk and posterior to the yolk mass as in other genera. Usually a narrow waist separates the adhesive array from the remainder of the trunk and in *Diplosoma* the waist tends to isolate the blastozooids from the oozooid. In *Leptoclinides* and *Polysyncraton* and sometimes in *Trididemnum* and *Didemnum*, a (usually large) finger-like horizontal accessory ampulla projects from the larval epidermis on the left, more or less from behind the adhesive array in the vicinity of the trunk waist, and extends anteriorly in *Leptoclinides* and posteriorly or vertically in *Didemnum*, *Polysyncraton* and *Trididemnum*. In larvae of *Atriolum* there is some variation in these accessory ampullae. They all project anteriorly from the waist behind the lateral ampullae but *A. lilium* sp. nov. has a short rounded projection on each side, *A. marinense* sp. nov. has a small short projection on the left, and *A. robustum* has 3 in a vertical row on the left. The accessory ampullae may be rudimentary stolonic vessels. Such accessory horizontal ampullae have not been detected in the larvae of either *Lissoclinum* or *Diplosoma*. Series of short-stalked papillae surround the anterior of the trunk in some *Lissoclinum* and in *Clitella*, although these never appear to separate off from the larval epidermis to form vesicles as they do in *Polyclinidae* and *Ritterellidae* (Kott, 1992a). The endostyle is short and vertical.

Larval pharynges in the oozooids of *Atriolum*, *Leptoclinides*, *Polysyncraton*, *Lissoclinum*,

Clitella and *Diplosoma* each have 4 rows of stigmata, but those of *Didemnum* and *Trididemnum* have 3. In the one species of *Trididemnum* in which they occur the blastozooids also have 3 rows of stigmata. In the other genera when they occur (occasionally in *Didemnum*, often in *Polysyncraton*, *Lissoclinum* and *Diplosoma*, but never in *Atriolum* or *Leptoclinides*) blastozooids have 4 rows of stigmata. In *Polysyncraton*, the adult organs take longer to develop than in most other genera. Larval trunks are relatively large and robust in *Leptoclinides* and *Atriolum* (about 1.0mm). *Didemnum*, *Polysyncraton*, *Lissoclinum* and *Diplosoma* with 2 or more larval blastozooids also tend to have a large trunk 0.5 – 1.0mm long. In *Trididemnum pseudodiplosoma* which has blastozooids (up to 7) the larval trunk is 1.2mm long. In some species without blastozooids the larval trunk is less than 0.5mm. In *Clitella*, with up to 7–8 blastozooids, the large antero-posteriorly flattened, disc-shaped larva is 2mm in diameter. Precocious budding to produce blastozooids before metamorphosis involves production of separate thoracic and abdominal buds from the oesophageal neck of the oozooid, apparently in the same way as in adult zooids. Most *Didemnum*, *Leptoclinides* and *Diplosoma* have a broad, oval larval trunk but in *Trididemnum*, *Lissoclinum* and *Polysyncraton* the trunk narrows posteriorly.

lateral organs: Spicules have a cellular origin in the thoracic lateral organs (Lafargue & Kniprath, 1978; Ballan-Dufrançais et al., 1995) — paired ectodermal invaginations into, or spoon-shaped or flap-like projections from, the parietal body wall, one on each side of the thorax. The test projects into the concavity of the lateral organ, and when this knob of test and spicules is pulled out it can evert the concave lining of the lateral organ and it changes an inverted pocket to a stalked projection. The lateral organs are usually on each side of the base of the atrial siphon when one is present or in species with open, sessile atrial apertures the lateral organ is on the edge of each side of the opening. However its precise location varies due to contraction of parietal and pharyngeal muscles.

In *Atriolum* and *Leptoclinides* the lateral organs are circular to oval saucer-like depressions in the parietal thoracic wall at each side of the base of the atrial siphon. In *Atriolum* they are 0.06–0.1mm diameter. In *Leptoclinides* most are 0.04–0.06mm diameter, although in *L. coelenteratus*, *L. cuspidatus*, *L. imperfectus*, *L. levitatus*, *L. longicollis*, *L. placidus*, *L. variegatus* and *L. rigidus* they are about 0.1mm diameter; *L. brandi* to 0.125mm, *L. confirmatus* to 0.225mm diameter; and *L. echinus* to 0.3mm diameter. *Trididemnum* spp. have saucer-like depressions in the parietal body wall (similar to *Leptoclinides*) at each side of the base of the atrial siphon, opposite the second interstigmatal vessel. They generally are 0.04–0.06mm diameter but in *T. sibogae* and *T. lapidosum* they are about 0.2mm diameter. In *Polysyncraton* the lateral organs are depressed into the parietal thoracic wall. They are found in the mid-thoracic wall between the first and third interstigmatal vessels and ventral to the lateral rim of the atrial aperture. Their maximum diameter is 0.04–0.06mm and they are deep, often spherical flask-shaped organs. The narrow opening to the exterior is directed ventrally.

In *Didemnum*, the lateral organs are ventral (each side of the endostyle). Many are large (max. diameter 0.05–0.08mm) oval to circular cup- or flask-shaped organs or pockets invaginated into the parietal thoracic wall with the opening directed ventrally; others are smaller (less than 0.05mm) spoon-shaped or simple flap-like projections from the body wall always with the concavity facing ventrally or postero-ventrally. Of the lateral organs detected, *Didemnum albopunctatum*, *D. arancium*, *D. caesium*, *D. candidum*, *D. chartaceum*, *D. clavum*, *D. cuculliferum*, *D. grande* and *D. viride* have invaginated flasks; *Didemnum astrum*, *D. effusium*, *D. etiolum*, *D. fuscum*, *D. incanum*, *D. jedanense*, *D. membranaceum*, *D. minisculum* , *D. multispirale*, *D. oblitum*, *D. patulum*, *D. pellucidum*, *D. perplexum*, *D. sordidum*, *D. spadix*, *D. uturoa*, *D. velatum* and *D. vahatuio* have projecting stalked spoon-shaped lateral organs; and *D. crescente*, *D. fragum*, *D. jucundum* and *D. lissoclinum* have flap-like projections. The lateral organs are opposite the first to the third interspace, but most often opposite the third row of stigmata. *Lissoclinum* has a range of lateral organs, from saucer-shaped invaginations 0.03– 0.125mm in diameter (the largest, *L. concavum* and *L. sente*) to spoon-shaped projections (*L. badium*, *L. bistratum*, *L. conchylium*, *L. patella* and *L. ostrearium*). The lateral organs in this genus are very close to the endostyle, and as in *Didemnum*, opposite the first to third interstigmatal vessel, usually opposite the second and third interspace or the third row of stigmata. In *Clitella nutricula* the lateral organ is a 0.1mm diameter saucer in

the parietal body wall opposite the fourth row of stigmata.

Lateral organs were not detected in the aspicular *Diplosoma*. Spicules are not known in the larval test of any taxon, and, with the exception of *Atriolum robustum* and *Didemnum fucatum*, lateral organs have not been observed in the larval pharynx.

lobulation: As well as replication of zooids and growth of the colonies, colonies of some species subdivide in a process known as lobulation (Cowan, 1981; Ryland et al., 1984; Ryland, 1989). This confers selective advantages and has ecological consequences associated with dispersal (Kott, 1982a). Having subdivided, the replicate colonies of certain species are known to move away from one another to space themselves. Other movements are toward the light. This movement and colony replication has been observed only in tropical *Didemnum molle* (see Birkeland et al., 1981; Cowan, 1981), and *Lissoclinum bistratum*, *L. voeltzkowi* (<*L. timorense*), and *Diplosoma virens* (see Ryland et al., 1984; Ryland, 1989, 1990), all with obligate symbiotic, single-celled, prokaryotic, chlorophyll-containing *Prochloron* Lewin, 1977 (Kott, 1980,1982a; Kott et al., 1984). The response to light of the didemnid colony apparently is determined by the photosynthetic requirements of the symbionts (Parry, 1987). Movement has not been reported either in other species of tropical Didemnidae with *Prochloron* symbioses, or in species with similar symbioses with cyanophytes (Parry, 1984a; Parry & Kott, 1988).

longitudinal pharyngeal muscles: see **muscles**

movement: see **lobulation**

muscles: Body musculature (confined to the thorax and sometimes extending onto the upper part of the oesophageal neck) consists of circular bands around the siphons, transverse pharyngeal muscles in the transverse bars of the branchial sac (between the rows of stigmata), a pair of (usually strong) dorsal longitudinal pharyngeal muscles in the pharyngeal wall along each side of the dorsal mid-line, some fine longitudinal bands in the parietal body wall of the thorax and, in *Atriolum*, some *Trididemnum* spp. and a few *Leptoclinides* spp. (*L. brandi*) only, some transverse bands have been detected in the parietal wall of the thorax. The longitudinal pharyngeal muscles are especially fine in *Atriolum*, *Leptoclinides* and *Lissoclinum*. The muscles in the transverse branchial vessels lie at the base of the flat transverse membrane that projects into the lumen of the pharynx and can be readily seen only in stained preparations of well relaxed thoraces. The transverse pharyngeal muscles are continuous across the dorsal surface beneath the dorsal longitudinal pharyngeal muscles but ventrally they break up into branches on each side of the endostyle and are dispersed into the body wall outside the endostyle. In *Atriolum* and some *Leptoclinides* some fine transverse parietal muscles cross the dorsum behind the atrial siphon and curve around it from each side. In *Leptoclinides* some oblique parietal muscles from along each side of the endostyle extend to the posterior end of the thorax more or less parallel to the more dorsally positioned longitudinal parietal muscles. In *Atriolum* and *Leptoclinides* the latter terminate, on each side, at the posterior end of the thorax, near the anus.

Always in *Trididemnum*, usually in *Didemnum, Polysyncraton* and *Diplosoma*, and occasionally in *Lissoclinum* the dorsal longitudinal pharyngeal muscle on each side extends ventrally across the posterior end of the thorax, is joined by longitudinal fibres from the parietal body wall and, ventral to the oesophagus, combines with the corresponding longitudinal muscles from the other side of the body to form a retractor muscle that, covered with a layer of ectoderm, projects away from the zooid, tapering as its fibres progressively terminate in the surrounding test. The length and thickness of the retractor muscle is related to its state of contraction and is not always a significant character for species determination. Some interspecific variation occurs in the level at which it separates from the oesophageal neck, although this is difficult to determine precisely. The anterior part of the oesophageal neck (where the longitudinal thoracic muscles join to form the retractor muscle) is the only part subject to contraction and, in contracted zooids, the proximal end of the retractor muscle is invariably drawn up toward the thorax. *Leptoclinides* and *Atriolum* never have a retractor muscle.

The oesophageal sphincter is an unusual muscle that appears to be developed in *Trididemnum* (sometimes in *T. cyclops*: Monniot & Monniot, 1987, below), *Diplosoma* (*D. ata* Monniot & Monniot, 1987 — although it is referred to as a fibrous ring), *Lissoclinum* (*L. nebulosum*), and *Didemnum* (*D. fucatum*, below). In each of these species, the muscle is similar, the fibres from the longitudinal dorsal pharyngeal and parietal muscles terminating in

this sphincter that encircles the oesophageal neck, rather than terminating in a retractor muscle. It is possible that it is associated with replication, which would explain its ephemeral occurrence in *T. cyclops*.

oesophageal sphincter: see **muscles**

pharyngeal muscles: see **muscles**

pharynx: see **stigmata**

projecting columnar cells: Crowded columnar ectodermal cells with rounded spatulate (e.g. *Polysyncraton dentatum* sp. nov., *P. meandratum*) or long attenuated (e.g. *P. infundibulum* sp. nov.) tips projecting vertically from the surface of the zooid are visible in mounted preparations of many didemnids. Similar projections on the body wall of *D. molle* were reported as scales (Kott, 1980), and their true nature was not recognised. They have been found often in *Polysyncraton* and *Didemnum*. In *Atriolum* and *Leptoclinides* they were detected on the thorax, especially around the base of the branchial siphon and on the siphon itself in *A. tubiporum* , *L. fungiformis*, and *L. umbrosus*; and over most of the body surface — both thorax and abdomen in *L. comitus*, *L. rigidus* and *L. volvus*. In *Polysyncraton* and *Didemnum*, almost without exception, tapering or rounded projecting cells are present, sometimes only around the anterior part of the thorax but occasionally over the whole zooid. Species in which they have not been detected in any of the specimens examined are *Didemnum grande* and *D. membranaceum* and *D. viride*. They were not detected in *Trididemnum*, including those species with dark squamous epithelium especially over the anterior part of the thorax and the branchial siphon; nor were they detected in *Diplosoma* in which many species have dark squamous epithelium over the whole body wall. In *Lissoclinum* conspicuous projecting cells are present on the thorax of *L. nebulosum*, *L. timorense* and *L. variabile*, although the latter species has dark squamous epithelium over the abdomen. *Clitella* has blunt and stalked club-shaped projecting cells over the whole thoracic and abdominal wall (Fig. 2). They appear not to have phylogenetic implications at genus level. They are found across the top of the thorax, on the branchial siphon, sometimes all over the thorax, along the rim of the atrial aperture, on the atrial tongue, around the top of the oesophageal neck, and sometimes on the base of the abdomen. Although they were detected especially on those parts of the zooid which could be expected to make a firm attachment to the test, such an attachment was not observed in the present study. These columnar cells appear to be physiologically active, each with a large nucleus clearly visible and they appear to have a functional physiological significance beyond a passive anchoring role. Little is known of either the ascidian epidermis or of the mechanisms by which the test is synthesised, beyond proposals that the ectoderm is involved, and it is not impossible that these columnar cells are involved in the process (Goodbody, 1974; Burighel & Cloney, 1997).

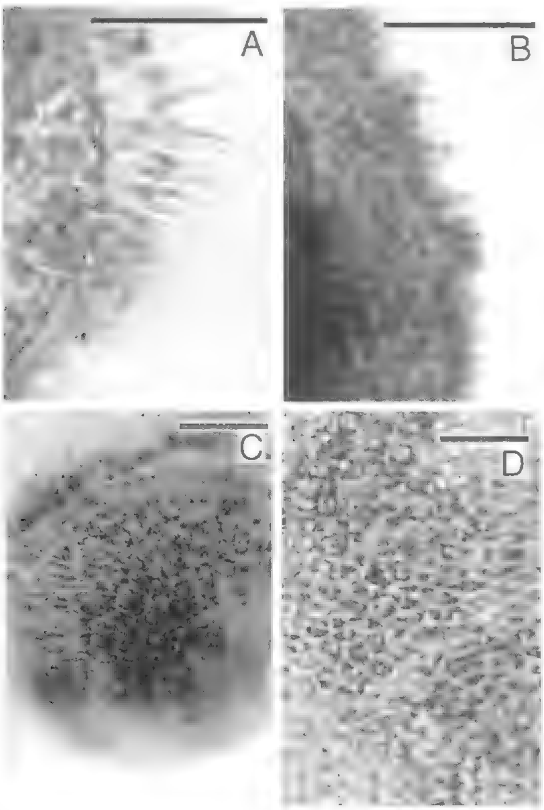


FIG. 2. Epidermal features A, B, Columnar cells projecting from the anterior thoracic wall — A, with tapering tips (*Polysyncraton infundibulum* sp. nov.). B, with rounded spatulate tips (*Clitella* gen. nov. *nutricula* sp. nov.). C, D, Squamous epithelial cells on abdomen — C, *Lissoclinum variabile* sp. nov. (QM G308008). D, *Diplosoma ferrugeum* sp. nov. (QM GH321). Scales 0.05mm.

rastrum: The rastrum is a T-shaped extension of the larval ectoderm and posterior haemocoelic cavity from the posterior end of the larval trunk just above the tail insertion. It carries algal cells in *Diplosoma/Prochloron* symbioses from one generation to the next. The larval test over the

rastrum is broken up into a brush of hairs which gather and enmesh plant cells as the larva, having been incubated in the basal test of the colony, breaks into the common cloacal cavity through the layer of plant cells that line it.

replication: Replication in the Didemnidae is by oesophageal budding, thought to be a form of horizontal strobilation similar to that in other Aplousobranchia, but with the thoracic and abdominal buds developing from the oesophageal region of the zooid before it divides. This is in contrast to all other aplousobranchs where division of the zooids occurs before regeneration of new parts (Berrill, 1935). Vestiges of the epicardial sacs (Kott, 1990a) remain in the oesophageal neck of didemnid zooids, and are involved in generation of the new thoraces and abdomina. The division of zooids across the oesophageal neck, separates 2 new zooids from one another, one being a thoracic bud with the parental abdomen, and the other an abdominal bud with the parental thorax. The process is particularly prolific in certain tropical species with symbiotic associations with *Prochloron*. Sometimes as many as 3 generations of buds are simultaneously associated with the parental zooids (*Diplosoma multipapillatum* Kott, 1980). Most of what is known of replication in the Didemnidae is based on *Diplosoma* (Caullery, 1895a,b; Hjort, 1896; Berrill, 1935). Oesophageal buds are frequently observed in *Didemnum*, *Trididemnum*, *Polysyncraton* and *Lissoclinum* and the process probably is similar to that in *Diplosoma*. Although oesophageal buds are only occasionally recorded in *Leptoclinides* (*L. fungiformis* and *L. erinaceus*), there is no reason to believe that the process is different from that in other genera of the family. However, the presence of whole zooids, of which both thorax and abdomen are juvenile, in the basal test of *L. levitatus* and *L. longicollis* together with terminal ampullae of test vessels, suggests that some other form of replication may occur in this genus in addition to oesophageal budding.

The precocious budding, that produces blastozooids in the larvae of certain species in all genera except *Atriolum* and *Leptoclinides*, is the same as in the adult — viz. the development of separate thoracic and abdominal buds from the oesophageal neck of the oozooid. Usually one thoracic bud is found in the larvae of a few *Didemnum* spp., and 1–3 in many *Polysyncraton* spp., *Lissoclinum* spp. and *Diplosoma* spp., in addition to abdominal buds. In *Trididemnum pseudodiplosoma*, the only species of the genus in which larval blastozooids develop, up to 7 thoracic and 5 or 6 abdominal buds are found. In *Clitella* (in which even more buds develop than in *T. pseudodiplosoma*) each successive blastozooid produces the next in the series, and the division of the parent blastozooid across the oesophageal neck occurs before metamorphosis and before the next set of buds develop so that a whole juvenile colony occurs in the larva.

Replication of the zooids is a phenomenon of growth, rather than reproduction. The growth of a didemnid colony appears to be particularly fast because the replicative process is efficient, the zooids continuing to filter water while the buds develop. Further, colony growth is 2- rather than 3-dimensional, the thin sheet-like colonies of so many species covering the substrate, and out-competing many other species, including juveniles of solitary ascidians (Goodbody, 1965).

retractor muscle: see **muscles**

seminal vesicles: The long vas deferens coiled around the testis (in all genera except *Lissoclinum*, *Clitella*, and *Diplosoma)* acts as a seminal vesicle, storing sperm before its release (Burighel & Martinucci, 1994a,b; Ryland & Bishop, 1990). In *Clitella* and *Diplosoma* the proximal part of the vas deferens, just where it leaves the posterior end of the testis and curves around its dorsal surface or between the 2 lobes of the testis, is often swollen into a large, club-shaped seminal vesicle.

spicules: Aragonite (Lowenstam & Wiener, 1989) spicules generated in the thoracic lateral organs, occur in all didemnid genera except *Diplosoma*. It is possible that an advantage of the white stellate calcareous spicules is to reflect light and shade the colonies in shallow tropical waters. They probably also strengthen the test. Didemnid spicules are diverse (Fig. 3A). Their size range and variety show little or no intraspecific variability. They are accordingly reliable indicators of species identity. Generally they are spherical (stellate, mulberry-like, globular, or burr-like) and composed of tightly packed radial rods of calcium carbonate. In stellate spicules the rods are of different lengths grouped together to form, a definite number of separate conical rays around the periphery of a central mass. Rays of any one of the stellate spicules usually are the same diameter, length and shape, although in a few species one or more of the rays may be enlarged creating an irregular or fusiform spicule. In mulberry-like spicules the rays are short and round-tipped. Globular

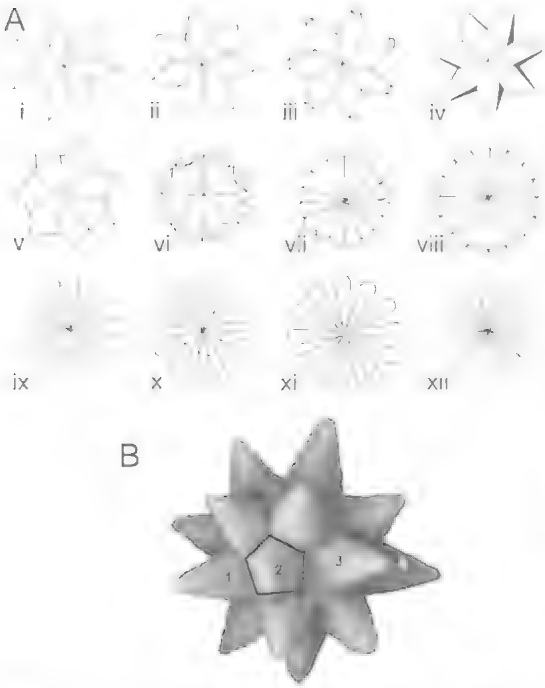


FIG. 3. A, types of spicules (diagrammatic) – Stellate; i, conical rays; ii, blunt-tipped rays; iii, truncated rays; iv, chisel-shaped rays. Globular; v, short points separated on central mass; vi, short points set in concave bases; vii, rounded tips or mulberry-like; viii, flat-tipped rays. Burr-like; ix, needle-like rays; x, rounded-tipped rod-like rays; xi, club or slate pencil urchin rays; xii, fusiform rays. B, Pentagonal arrangement and recording of spicule rays (semi-diagrammatic) — the spicule represented has 4 rays around its diameter on one side. Only rays corresponding to 1, 2 and 3 appear to be present on the other side. The number of rays in optical transverse section will be recorded as 7.

spicules have flat-tipped rays crowded together around the surface, burr-shaped ones have pointed or flat-tipped rod-like or fusiform rays that are not crowded together on the surface of the spicule. In some *Lissoclinum* spp. spicules have long pencil-like rays of different lengths graded to form spicules with flattened diamond or triangular or plate-like outlines or with 3 or 4 long arms. In a few cases the conical pointed tip of each spicule ray appears to be set in a concavity (usually pentagonal) either in the solid central mass, or in the end of a short wider basal section of the ray.

Although spicule type seems to be genetically determined at species level, it is not a significant generic character. There are, however, certain spicule types which do occur more often in certain genera than in others. Large stellate spicules, often with chisel-shaped and/or truncated ray tips, occur in a majority of *Atriolum*, *Leptoclinides* and *Trididemnum* species, although some species with burr-like spicules do occur in *Leptoclinides* and *Trididemnum*. Burr-like spicules predominate in *Lissoclinum* and *Polysyncraton;* and in the former genus many species with rays fused and of different length occur to convert their basic spherical shape from radial to bilateral symmetry. Nevertheless species with the usual stellate shapes also do occur in both *Lissoclinum* and *Polysyncraton*. The diverse genus *Didemnum* has representatives of all spicule types and in many species more than one.

Arrangement of spicule-rays is roughly pentagonal, any one ray being surrounded by 5 others. This is more obvious in spicules with fewer rays. The arrangement is not geometrically precise (Fig. 3B). Spicules of all sizes up to the maximum diameter characteristic of the species, are usually adequately sampled in a 5mm strip of test, although when sparsely distributed a larger amount may be needed. The largest spicules known are those of *Leptoclinides magnistellus* from Tasmania which reach 0.24mm diameter. More often spicules are up to 0.1 to 0.15mm in diameter in a number of *Leptoclinides* spp. and *Trididemnum* spp., and although spicules of this order also occur in *Didemnum* spp., *Polysyncraton* spp. and *Lissoclinum* spp., most species in those genera have a smaller maximum spicule diameter. Apart from these general trends, spicule size has no phylogenetic implication.

squamous epithelium: In some members of this family dark squamous epithelium is present over the abdomen and often also the thorax. In *Diplosoma*, it is usually present over both abdomen and thorax. In *Trididemnum* (*savignii* species group) similar dark epithelium is present on the branchial siphon and thorax. It is present only rarely, and only on the abdomen in *Didemnum* (*D. albopunctatum*), *Lissoclinum* (*L. variabile*) and *Polysyncraton* (*P. orbiculum*).

stigmata: The size of the zooids, from the largest in *Atriolum* reducing progressively (though without implying a linear relationship) through *Leptoclinides*, *Lissoclinum Diplosoma*, *Polysyncraton* and larger *Trididemnum* to the smallest zooids of *Trididemnum* and *Didemnum*, is reflected in the size of the branchial sac, and the related numbers and length of the stigmata. Always the numbers of stigmata per row are

greater in the anterior row, reducing by up to 3 or 4 in the posterior row. The maximum number of stigmata per row (on one side of the body) is 15 –25 in *Atriolum*, 12 –20 in *Leptoclinides*, 8 – 14 in *Polysyncraton* and *Lissoclinum*, and 6 – 12 in *Diplosoma* while in *Didemnum* the anterior row usually has from 5–10 stigmata. The greatest range in the number of stigmata is in *Trididemnum* where they range from 5–6 in the anterior row of the smallest species (such as *T. clinides*) to 16 in the large *T. lapidosum*. Similar numbers of stigmata are be found in well-developed thoracic buds and larval pharynges as in the adult zooid.

Epithelial cells lining the stigmata are low and flat along each side while the shape of the opening is determined by the cells at each end which increase in depth as they approach the extremity. Fusiform stigmata (e.g. *Leptoclinides brandi* sp. nov.) have a single deep diamond shaped cell in the pointed tip at each end. In those stigmata that are rectangular these terminal cells are themselves more regularly cuboidal, while in the majority of species the cells in the extremities of each perforation gradually increase in depth toward the end of the opening to form a shallow crescent around it. The large epithelial cells at each end of the stigmata appear to stabilise each end of the perforation and maintain the shape of the opening.

Large imperforate spaces are at the anterior and posterior ends of the pharynx in all genera and in most species. In *Trididemnum* these spaces are particularly extensive. A retropharyngeal groove joins the posterior end of the endostyle to the oesophageal opening.

stolonic vessels: The 2–3 stolonic (ectodermal) vessels projecting from the abdomen of each zooid, each ending in a slightly expanded terminal ampulla with enlarged epithelial cells around the distal tip, occur in all genera but often are inconspicuous. Sometimes they are short and stumpy, but especially in *Diplosoma* they may be very long, extending out into the test, and in some species their rounded terminal ampullae can be seen in the base and around the margins of the colony. These vessels appear to be the homologues of the vascular appendage of Holozoidae, but not of the vegetative stolon in the same family. They may also be homologous with the small vascular appendages that arise from the posterior end of the zooid in Polycitoridae, Polyclinidae, and other aplousobranch families. They also resemble, and may be homologous with the test vessels of stolidobranch and phlebobranch ascidians. Millar (1951) refers to an anterior origin for these vessels near the oesophageal buds but their association with the oesophagus is only apparent. Their origin is always posterior to the oesophageal buds, from the body wall on the ventral side of the gut loop — the side opposite the gonads. They are not always reported partly because of their origin from inside the ventral concavity of the gut-loop flexure and partly because of their small size or their delicacy. They often break off when zooids are removed from the test and the inconspicuous part of the vessel remains in the test, obscured by the embedded spicules. Lahille (1890) suggested a tunicin secreting function for the terminal ampullae — a suggestion supported by Millar (1951) who studied these vessels in a species each of *Lissoclinum*, *Diplosoma*, *Didemnum* and *Trididemnum*.

substrates: The substrates to which didemnid colonies attach are generally cryptic, clean and well scoured under or vertical surfaces rather than upper surfaces on which sediments settle; or larger colonies in benthic seafloor habitats tend to develop vertical, upright forms with terminal excurrent apertures that divert sediments from their upper surfaces. Exceptions are a few species, all with obligate symbioses with plant cells, which occur free on the sandy sediments of reef flats, viz. *Lissoclinum bistratum*, *L. patella* and *L. timorense*. These have sandy particles attached to the base of the colony.

symbioses: Obligate algal symbionts of Didemnidae either are embedded in the test, or line the walls of the cloacal cavity. Although *Prochloron* is found in both locations, depending on the host species, cyanophytes are only found embedded — they are never found in the cloacal cavity (Parry, 1984a; Parry & Kott, 1988). *Prochloron* cells in the cloacal cavity are held firmly to its walls, partially embedded in the test (Newcomb & Pugh, 1975; Hirose et al., 1996). The symbionts are not readily dislodged from living specimens, although living colonies of *D. molle*, when disturbed, release *Prochloron* from the cloacal apertures in streams of mucus. In the case of obligate symbioses, the symbiotic ells are carried from the parent to the new colony that will develop (Kott, 1980, 1982a, b) either by adhering to the posterior end of the larval trunk, or by forming a coat around it leaving ‘windows’ over the sensory and adhesive organs, or rastrum (see above). Non-obligate symbionts are usually on the surface of the test, occasionally in the cloacal cavity and are readily removed. Obligate

didemnid-*Prochloron* or cyanophyte relationships are not monophyletic. They occur in *Didemnum*, *Trididemnum*, *Lissoclinum* and *Diplosoma*. Monniot (1993) reported unicellular plant cells in *Polysyncraton multipapillae* from New Caledonia, although these are not known to be *Prochloron*; nor is it known to be an obligate association. Otherwise, only non-obligate symbioses are reported in *Polysyncraton*, *Leptoclinides* (e.g. *L. dubius*, *L. brandi*, below; Kott, 1980, 1982a) and *Atriolum* (*A. marinense*). Ascidian taxa other than didemnids form only non-obligate symbioses with plant cells, and in some cases with prokaryotic plant cells, including *Prochloron* (see Kott et al., 1984). Apart from the prokaryotic cells in these obligate symbioses, there are no inclusions such as sand or other foreign particles embedded in the test of Didemnidae except faecal pellets in *D. psammatode* and a chlorophyte as well as cyanophytes in *T. clinides* (Parry & Kott, 1988).

Hirose et al. (1996) reported phagocytosis of *Prochloron* symbionts by test cells of *L. punctatum* Kott, 1977as evidence of a stable intracellular endosymbiosis that constitutes a model for the evolution of the ancestral green plastid. This phagocytosis must be interpreted in the context of the morphology and biology of *Lissoclinum punctatum*. In undisturbed colonies *Prochloron* cells are in the common cloaca and are not normally in the test. The phagocytosis probably is a response to *Prochloron* cells invading the test around the common cloacal cavities when these delicate colonies are disturbed. Although the engulfed *Procholoron* appear healthy, their ultimate fate was not observed, and they were not found to be numerous. (See also **substrates, rastrum**).

test synthesis: see **projecting columnar cells**

test inclusions: Generally foreign bodies such as sand or rubble, are not included in the test in Didemnidae although some massive colonies contain such particles when parts of their basal surface with adherent particles are folded in, or overgrown by the colony (see above **substrates**). Faecal pellets crowd the test of *D. psammatode* but otherwise are reported only in the base of the colonies of *D. stercoratum* Monniot & Monniot, 1996 and *T. savignii* (below). Chlorophyll-containing symbionts also are in the test of some species (see, **symbioses**). A strongly acid reaction has often been observed in the test of didemnids. This results from lysis of cells. It is not an intercellular or intracellular condition of undisturbed colonies in situ; the acid generated is rapidly neutralised in seawater, and presumably by the calcareous spicules (Parry, 1984b).

testis: The testis is found against the dorsal side of the post-pyloric distal part of the gut loop. When the gut loop is flexed ventrally, or bent up to form a double loop, the test maintains its position in regard to the gut loop and is at the posterior end of the zooid. The testis is undivided and dome-shaped, oval or conical in *Atriolum*, *Trididemnum*, usually in *Didemnum* and in a few species of *L. faroensis* Bjerkan, 1905 from the North Atlantic, *L. capensis* Michaelsen, 1934 from South Africa, and *L. unitestis* Monniot, 1989 from New Caledonia but in most *Leptoclinides* (with *L. faroensis* the only exception) and *Polysyncraton* it is divided into a number of club-shaped follicles, usually not more than 8–9, arranged in a circle, except in the *dubius* species group where testis follicles are in a grape-like cluster of about 20. In a few *Lissoclinum* species testis follicles are also in a grape-like cluster, although more often the testis is undivided or divided into 2 as in *Diplosoma* and *Clitella*. A number of *Didemnum* spp. also have the testis divided into 2. In this case, the vasa efferentia join the vas deferens in the centre of its spiral around both lobes, not at the posterior end of each lobe as it does when the vas deferens is straight. (See also, **vas deferens**).

vascular appendages, — **stolons**: see **stolonic vessels**.

vas deferens: The cone or dome-shaped undivided testis (in *Atriolum*, a few *Leptoclinides*, most *Didemnum* and all *Trididemnum*) narrows abruptly to the vas deferens in the centre of its parietal side (the base being against the gut loop). When divided into follicles (in most *Leptoclinides* and *Polysyncraton*) they narrow and converge to the same point. From its point of origin on the outside of the testis, the vas deferens coils around the testis in all genera except *Diplosoma*, *Lissoclinum* and *Clitella*. Although a range in the number of vas deferens coils has invariably been reported this appears to result from the difficulty in distinguishing the number of coils as they lie closely on the testis (Fig. 4). In the present study, the number of coils has been found to be a species characteristic, only rarely subject to intraspecific variation. Such variations occur only in certain *Polysyncraton* spp. where the developing egg inside the outer coil of the vas deferens pulls it out as the egg increases in size .

The coiled vas deferens may have its genesis in the evolutionary reduction in length of the

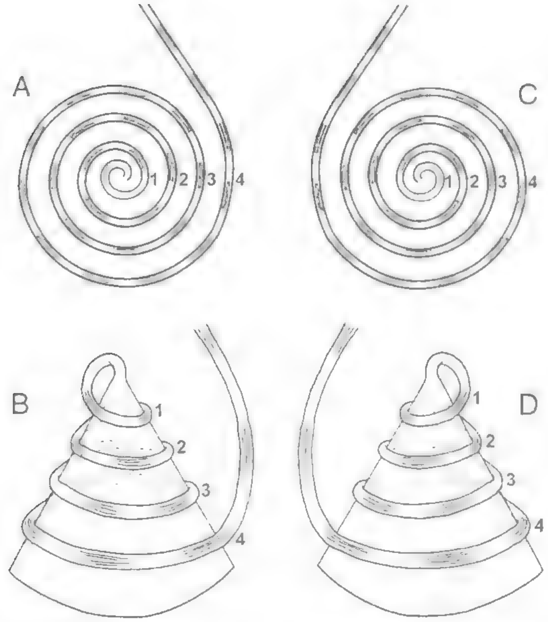


FIG. 4. Coiling and recording of the spiral vas deferens (diagrammatic). A, B, anticlockwise coil from above and posteriorly, respectively; C, D, clockwise coil from above and posteriorly respectively.

abdomen, the long duct being retained as a seminal vesicle. The direction of coiling of the vas deferens (clockwise or anti-clockwise) is variable, even in the colony, although in *Polysyncraton* it is most often coiled anticlockwise. In *Diplosoma*, *Clitella* and usually *Lissoclinum* the testis is divided into two parallel lozenge-shaped lobes or is spherical and undivided. The vas deferens hooks around from the posterior end of the undivided testis and extends anteriorly over its parietal surface or, from the posterior ends of the two contiguous lobes of the divided testis, it extends anteriorly in the dorsal part of the groove between them. In *Lissoclinum* and *Clitella* , the proximal part of the vas deferens is expanded into a large seminal vesicle, compensating for the lack of a coiled (longer) duct.

TAXONOMY

KEY TO GENERA OF THE DIDEMNIDAE

1. Vas deferens coiled 2
   Vas deferens not coiled 6
2. Stigmata in 3 rows . . . . *Trididemnum*
   Stigmata in 4 rows 3
3. Atrial siphon present, aperture always posteriorly directed; always without a retractor muscle 4
   Atrial siphon not present, aperture usually not posteriorly directed; usually with a retractor muscle 5
4. Atrial siphon at least as long as the thorax; common cloacal cavity an uninterrupted central chamber *Atriolum*
   Atrial siphon less than the length of the thorax; common cloacal cavity not an uninterrupted central chamber . . . . *Leptoclinides*
5. Testis divided into more than 2 follicles; vas deferens coils loosely. . . . . *Polysyncraton*
   Testis undivided or divided into 2; vas deferens coils tightly. . . . . *Didemnum*
6. Spicules usually present in test; sometimes with more than 2 testis follicles. 7
   Spicules not present in test; never with more than 2 testis follicles . . . . *Diplosoma*
7. Larval adhesive cones present . . . . *Lissoclinum*
   Larval adhesive cones not present . . . *Clitella* gen. nov.

Genus **Atriolum** Kott, 1983

TYPE SPECIES. *Atriolum robustum* Kott, 1983.

Zooids are relatively large for the Didemnidae, thorax and abdomen together (excluding the very long posteriorly oriented atrial siphon) up to 5mm long. Cloacal systems lack secondary canals and are unlike those in any other didemnid. Always, the 5-lobed atrial aperture is on a long, posteriorly projecting siphon, opening directly onto the side of the zooid-bearing layer of test opposite to the 6-lobed branchial apertures. *A. lilium* has open saucer to cup-shaped surface concavities, each representing a cloacal cavity. In *A. eversum* the colony is completely everted with the branchial apertures in the central cavity and the atrial apertures around the outside. Four of the known species form upright single or branched tubes or flasks, each with a terminal common cloacal aperture and a large, roomy central cloacal chamber. The other two known species form irregular colonies with randomly placed common cloacal apertures. In all species the colonies are fixed by a limited number of characteristic short, rigid, tapering, prop-like attachment processes which adhere to the substrate at their distal tips and possibly support the colony above it.

A spherical and undivided testis has the vas deferens coiled either clockwise or anticlockwise around it. Embryos are incubated in a brood pouch attached by a narrow neck to the dorsum of the thorax, just behind the atrial siphon. The eggs reach the brood pouch through the oviduct. Sometimes (presumably after fertilisation) the brood pouch is detached and lies free in the test. Known larvae have a trunk 1–2mm long, 4 lateral ampullae 3 median adhesive organs, an ocellus and an otolith and 4 rows of long, relatively numerous stigmata.

Calcareous spicules in the test are stellate with numerous points, the majority not more than 0.04mm in diameter, although in *A. eversum*, *A. lilium* and *A. tubiporum*, some are larger (up to 0.1mm diameter).

Unlike many other genera of this family, *Atriolum* zooids have conspicuous transverse muscles in the parietal body wall as well as in the transverse vessels. The transverse pharyngeal muscles are continuous over the dorsal mid-line beneath the fine, inconspicuous paired dorsal longitudinal pharyngeal muscles which terminate in the body wall near the anus. There is no retractor muscle. The long atrial siphon has circular muscles parallel to those crossing the dorsum between the siphons. Distal to the spherical stomach, the gut is subdivided into the usual long duodenal area, oval posterior stomach in the pole of the loop and rectum. The latter has a constriction about halfway up (more or less level with the posterior end of the stomach) surrounded by particularly conspicuous tubules of the intestinal gland. The distal part of the almost horizontal gut loop usually bends ventrally to form an obtuse angle with the longitudinal axis of the zooid. The heart is in the abdomen, at the side of the gut loop. Unlike all other Didemnidae except *Leptoclinides* (see Hawkins et. al., 1983b), *Atriolum* contains vanadium, concentrations of 350ppm being found in *A. robustum*.

Kott (1983) discussed the similarity of the zooid of *Atriolum* to that of *Hypodistoma deerratum* (> *Sigillina deerrata*) and *H. fantasianum* (Kott, 1990a). Monniot (1989) dismissed any hypothesis of a phylogenetic relationship on the grounds that brood pouches occur in genera of other families (e.g. Pseudodistomidae). She argues that *Sigillina* (and presumably *Hypodistoma* as well) is more closely related to *Eudistoma* than to other holozoid genera, that therefore the brood pouch in *Sigillina* occurs independently of the holozoids. She therefore concluded that a brood pouch always occurs as an independent apomorphy. Monniot's arguments are invalid: *Sigillina* and *Eudistoma* have little in common except 3 rows of stigmata and independently opening 6-lobed apertures. The relationship of *Sigillina* with the Holozoidae (rather than Polycitoridae) is based on body musculature and role of the vegetative stolon rather than the number of rows of stigmata (Kott, 1990a). Further, even though a brood pouch may have evolved independently in one or another taxon (including *Atriolum*), this does not mean that it is an apomorphy in all the taxa in which it occurs. The overall similarity of the zooids of *Atriolum* and *Hypodistoma* (not just the brood pouch as Monniot implies), as well as their large larvae of similar size, could be the result of convergence associated with the posterior abdominal position of the cloacal cavity in both taxa. Nevertheless, the possibility of a common ancestor for Holozoidae and Didemnidae (before the replicative stolon of the Holozoidae evolved) should not be entirely dismissed.

Atriolum, like *Leptoclinides*, has inconspicuous dorsal pharyngeal muscles, terminating at the posterior end of the thorax, and like *Leptoclinides* it lacks a retractor muscle, and has large zooids with posteriorly directed atrial siphons. Monniot (1989) believed the brood pouch to be the sole distinction, separating *Atriolum* from *Leptoclinides*. It has, however, longer atrial siphons and a combination of other characters, some of which are in other didemnids but occur together in *Atriolum*. Like *Trididemnum*, most *Didemnum* and a few *Leptoclinides*, *Atriolum* has an undivided testis. Certain *Leptoclinides* spp. (e.g. *L. coelenteratus* and related species) have 5 small atrial lobes and atrial apertures opening directly into cloacal chambers as in *Atriolum*. However, in *Leptoclinides* cloacal chambers are terminal rather than central, there are secondary canals and horizontal cavities as well as the primary cavity, and the atrial siphon is shorter than in *Atriolum*. Also, although *L. marsupialis* and *L. brandi* have brood pouches, the embryos are incubated in the layers of basal test beneath the cloacal spaces, while in *Atriolum* a single layer of test surrounding a single large central cloacal chamber contains both developing embryos and zooids. Finally *Atriolum* has relatively low concentrations of vanadium (350ppm), an element that is present in *Leptoclinides* in concentrations of 8,000 – 10,000ppm (Hawkins et al., 1983).

Leptoclinides unitestis Monniot, 1989 from New Caledonia has zooids and spicules similar to those of *Atriolum marinense*, viz. 18 stigmata in each of its 4 rows (an unusually high number for *Leptoclinides*), an undivided testis, a large larva (trunk length 1.5mm), and large spicules (in the vicinity of 0.1mm diameter). Nevertheless it differs from *Atriolum* in having numerous cloacal apertures and only a short atrial siphon.

Coelocormus Herdman, 1886 has a colony similar to *Atriolum*, although its numerous male

follicles suggest that it is more likely a synonym of *Leptoclinides*.

Leptoclinides marsupialis (Monniot, 1989) from New Caledonia, first assigned to *Atriolum*, differs in having the testis divided into 5–6 male follicles, cloacal canals rather than a large central cavity receiving the smooth-rimmed atrial apertures on short siphons, and embryos in brood pouches that separate from the thorax and are incubated in the basal test. The species also has fewer thoracic muscles than *Atriolum*. It appears similar to *L. brandi* in which embryos rupture into the test from the top, rather than from the base of the abdomen, and in which there is a functional oviduct through which the ovum moves to the top of the abdomen as in *Atriolum*. It is possible that the brood pouch in these species indicates a common ancestry for *Leptoclinides* and *Atriolum*, the character persisting always in *Atriolum*, but only occasionally in *Leptoclinides*.

Atriolum is known only from 6 Indo-West Pacific species and only *A. marinense*, *A. robustum* and *A. tubiporum* are known from more than a single specimen. Gonads, including characteristic undivided testes, are known for all except *A. tubiporum* and *A. eversum*. The last 2 species are also the only ones in which thoracic brood pouches with embryos have not been observed.

KEY TO SPECIES OF *ATRIOLUM* FROM AUSTRALIAN WATERS

1. Atrial apertures in central concavity 2
   Atrial apertures around outside of colony . . . . *A. eversum* sp. nov.
2. Colonies consist of only one cloacal system . . . . *A. marinense* sp. nov.
   Colonies consist of several cloacal systems 3
3. Cloacal apertures constricted, regular, circular openings; cloacal cavities enclosed . . . . . *A. tubiporum* sp. nov.
   Cloacal apertures not constricted, regular, circular openings; cloacal cavities more or less open 4
4. Cloacal apertures with flaring rims 5
   Cloacal apertures without flaring rims . . . *A. robustum*
5. Spicules with long pointed rays; ray length/spicule diameter ratio >0.2 . . . . *A. bucinum* sp. nov.
   Spicules with short, blunt rays; ray length/spicule diameter ratio not >0.2 . . . . *A. lilium* sp. nov.

Atriolum bucinum sp. nov.
(Figs 5, 157D; Pl. 1A)

TYPE LOCALITY. Western Australia (Houtman's Abrolhos, Wallabi Group, coll. C.Bryce 1994, holotype QM G304670).

COLONY. The large colony, about 8cm high, consists of a tall central trumpet or vase-like structure, with a central cloacal chamber flared out at the top. Two smaller but otherwise vase-like lobes, one on each side, and each a single system, branch from the central vase. Each cloacal chamber is lined by a layer of evenly but sparsely distributed spicules. Externally a layer of crowded spicules meets the lining of the cloacal cavity (with its sparse spicules) in a sharp line around the flared rim of the cloacal opening, which is turned back around the outside of the colony. Spicules are relatively sparse in the internal test. Atrial openings into the central cavity, are each marked by 5 clusters of spicules in the siphon lining. Spicules are large (to 0.1mm in diameter), with long, acutely pointed conical rays, 9–11 in optical transverse section and ray length/spicule diameter ratio about 0.25mm.

The living colony is opaque red. Although the colour is lost in preservative, the colony remains opaque.

ZOOIDS. Zooids are about 6mm from the tip of the long atrial siphon to the rim of the relatively short branchial siphon. A strong, branchial sphincter is present around the branchial siphon. The atrial siphon is in line with and is about the same length as, the dorsal border of the thorax. The short abdomen projecting from the posterior end of the thorax at right angles to its longitudinal axis, is bent up to the right of the posterior end of the thorax. Fine longitudinal muscles extend along the length of the thorax, and are crossed by transverse muscles. The circular muscles along the length of the atrial siphon are parallel to the longitudinal parietal muscles. Fourteen stigmata with rounded ends are in the anterior row, behind the wide unperforated band at the anterior end of the pharynx. Twelve stigmata are in the second, 10 in the third and 8 in the last row of the branchial sac. Wide transverse vessels alternate with the rows of stigmata.

The relatively short gut loop has the usual almost spherical stomach, long duodenum, oval posterior stomach and wide rectum with a distinct proximal elbow and narrow constriction about halfway up, to which tubules of the gastro-intestinal gland are closely applied. The only available colony of this species does not have mature gonads or developing larvae.

REMARKS. The large flaring rims around the common cloacal apertures resemble *A. lilium*. The present species differs in its opaque, red colour, tall vase-shaped colonies with a deep rather than shallow central cavity and generally

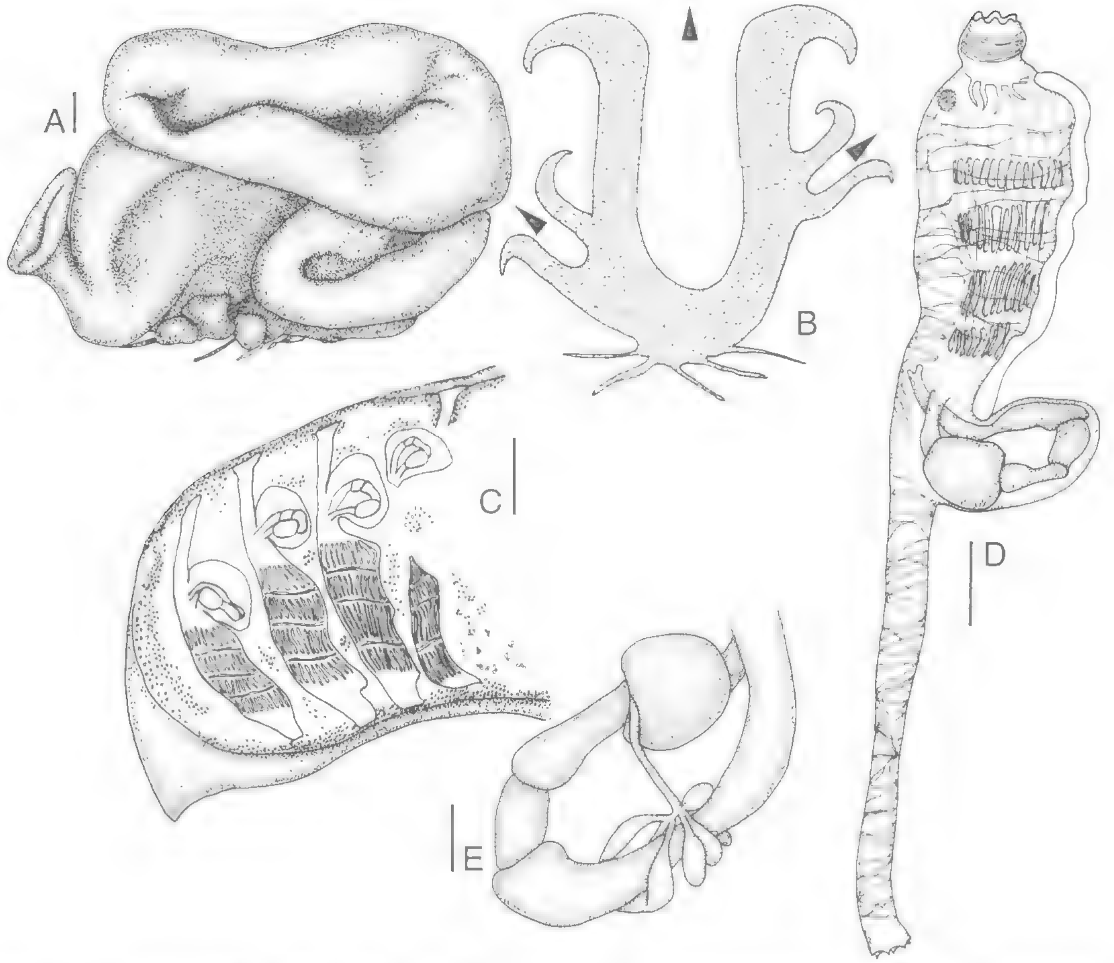


FIG. 5. *Atriolum bucinum* sp. nov. (QM G304670) – A, colony; B, diagrammatic vertical section through colony; C, semidiagrammatic transverse section through part of flaring everted rim of the common cloacal opening showing positions of spicules and zooids, with branchial apertures on the external surface and the atrial apertures on the everted border of the cloacal cavity; D, zooid showing long atrial siphon; E, gut loop showing gastro-intestinal gland. Scales: A, B, 1.0cm; C, 1.0mm; D, 0.5mm; E, 0.2mm.

larger spicules (those of *A. lilium* rarely exceeding 0.06mm diameter).

Atriolum eversum sp. nov.
(Figs 6, 157G)

TYPE LOCALITY. Western Australia (Houtmans Abrolhos, SW of Split I., Morning Reef, Wallabi Group, 180m, coll. L. Marsh 10.4.78, holotype WAM 366.80).

COLONY. The colony, a firm, upright, laterally compressed cup with a smooth, even surface, is 2cm long and about 1cm high. A concavity about 0.5 cm deep extends along the length of the upper surface. Spicules are up to 0.1mm diameter, with sharply pointed conical rays, and crowded throughout the test. Six-lobed branchial apertures are in dimples in the test lining the upper cavity. Conspicuous atrial apertures are around the outer surface of the colony, a double row of spicules projecting into the opening alternating with 5 narrow, pointed tongues around the rim of each.

ZOOIDS. Zooids are relatively large, the thorax about 3mm long, and the abdomen much less. Short but robust branchial siphons have conspicuous and sharply pointed lobes. Long (at least 2mm) posteriorly oriented atrial siphons stretch across to the outer surface of the colony. Of about 16 longitudinal muscles that terminate at the posterior end of the thorax, approximately 10 extend from the branchial siphon and the others extend across the dorsal surface behind the

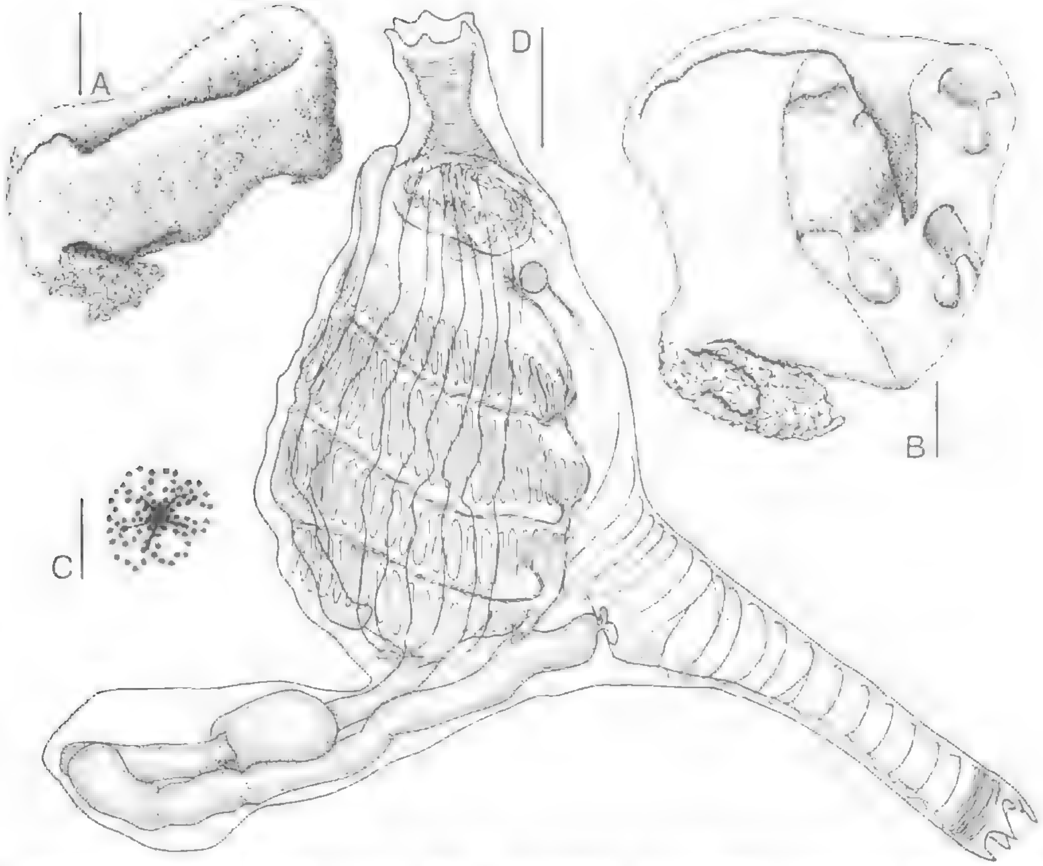


FIG. 6. *Atriolum eversum* sp. nov. (WAM 366.80). A, colony; B, semidiagrammatic vertical section through colony; C, spicules in test over the branchial lobes and in the siphonal lining; D, whole zooid. Scales: A, 5mm; B, 1.0mm; C, D, 0.5mm.

neural complex anterior to the base of the atrial siphon. The latter are the proximal bands in the series of parallel circular muscles that surround the atrial siphon. Sphincter muscles surround the base of the branchial siphon and the distal tip of the atrial siphon (just behind the lobes on the rim of the aperture). The conspicuous neural complex, consists of a spherical ganglion and a short curved duct from the neural gland on its ventral surface to a simple opening into the pharynx. A small lateral organ is opposite the posterior row of stigmata each side of the base of the atrial siphon. About 12 long branchial tentacles are at the base of the branchial siphon. 23 long fusiform stigmata pointed at each end are in each of the 4 rows. The long, pointed dorsal languets are on the transverse vessels to the left of the dorsal mid-line.

The narrow gut loop is almost vertical in some specimens, although in others it is open and bent ventrally. A post-pyloric duodenal area with a rounded, bulbous distal end opens into an oval posterior stomach. The gut abruptly increases in diameter at the proximal end of the rectum (in the pole of the gut loop). A conspicuous constriction is halfway up the ascending limb of the gut loop, where it is surrounded by tubules of the gastro-intestinal gland. The bilabiate anal aperture opens into the base of the atrial cavity. Gonads and larvae are not known.

REMARKS. The cloacal system appears to have developed a stage beyond that in other species of *Atriolum*, the atrial apertures opening around the outer surface rather than in an internal cavity or a concavity on the upper surface. It is as if the more usual closed cloacal cavity (as in *A. marinense* and *A. robustum*) was opened to the surface (as in *A. lilium*), and the whole colony subsequently turned inside out to achieve this colony form in which the oral surface has become concave and

enclosed and the excurrent pores are on the outer surface (Fig. 6).

Apart from differences in the cloacal system this species resembles others in this genus, with particularly large zooids and long, narrow atrial siphons with conspicuous 5-lobed apertures. It has more stigmata and larger spicules than other species in the genus.

Atriolum lilium sp. nov.
(Figs 7,157B; Pl. 1B)

TYPE LOCALITY. South Australia (eastern Great Australian Bight, Flinders I., Investigator Group, in caves with predatory cymatid mollusc, coll. N. Holmes Photo Index PE0036 R951 10.4.83, holotype QM GH2385).

FURTHER RECORDS. Indian Ocean (Great Australian Bight 33°14.5'S 126°20'E 183-192m, coll. El Tanin statn 2276, USNM 16406).

COLONY. The tough, robust holotype, about 5cm long has 2 large, concavities along the upper surface, each reminiscent of the inside of an open lily and homologous with a cloacal chamber. A conspicuous bladder cell layer is not present on the external surface, and a distinct line or rim is around each concavity where its test lining with evenly but sparsely distributed spicules meets the spicule-crowded surface test of the remainder of the colony. Only few scattered spicules are in the slightly translucent internal test.

The lining of each concavity is pierced by 5-lobed atrial apertures, with double rows of spicules continuing into the siphonal lining between the lobes. Six-lobed branchial apertures open to the exterior around the external surface, being absent only where a few short stumpy attachment processes, which appear to have raised the colony above the substrate, project from the under surface. As in all species of this genus the zooids stretch between atrial apertures into the internal chamber and branchial apertures on the outer surface of the colony.

Stellate spicules with 11 to 13 conical rays in optical transverse section and ray length/spicule diameter ratio from 0.15 to 0.2 are up to 0.1mm diameter, although the majority are only about half that size.

ZOOIDS. Zooids, relatively small for this genus, have a thorax about 1.5mm long, and a slightly shorter abdomen. A very long atrial aperture reaches to open by its 5-lobed aperture into a concavity on the upper surface. Branchial apertures have 6 sharply pointed lobes. Longitudinal muscles extend the length of the thorax, circular muscles with a sphincter at its tip surround the atrial siphon. A sphincter muscle also is present at the base of the branchial siphon. The dorsal ganglion is conspicuous, and a short curved neural duct opens into the pharynx by a simple opening. Large triangular dorsal languets are on the transverse vessels to the left of the mid-line. About 14 stigmata are in each of the 4 rows in the branchial sac.

The abdomen, bent up alongside the thorax has an open gut loop with the post-pyloric part bent ventrally. Occasionally, in this specimen, it is a tight, straight loop. The stomach is large, and a short, thick, cylindrical duodenum is separated from a small oval posterior stomach by a constriction. The wide rectum is also sharply constricted off from the distal end of the posterior stomach. Branching tubules of the gastric gland cluster around the ascending limb of the gut loop about halfway up the rectum.

Gonads are in the holotype. The testis is entire and is surrounded by 4 coils of the vas deferens spiraling in a clockwise direction in all the examined zooids. The testis is mature and obscured by a large ovum, with a conspicuous oviduct. Embryos, in brood pouches constricted off from the thorax near its posterior margin at the base of the atrial siphon, are against the wall of the cloacal cavity, into which they probably are liberated.

The larval trunk, 1.0mm long, with the tail wound two-thirds of the way around it, has 4 large, rounded lateral ampullae along each side of the 3 large relatively short stalked antero-median adhesive organs. On each side, a short, rounded accessory ampulla projects forward from the larval waist at the base of the lateral ampullae. A small ocellus and an otolith are in the cerebral vesicle, and 4 rows of stigmata have 11 stigmata in the anterior row and the numbers in each row progressively reduced to 8 in the posterior row.

REMARKS. The species is distinguished by its large open, flaring cloacal apertures, large size range of spicules and relatively small zooids with fewer stigmata than most other species. The shape of the spicules, attachment processes from the base of the colony, long atrial siphons with 5-lobed apertures, thoracic brood pouch and single male follicle are characteristic of the genus.

The species most closely resembles *A. bucinum* and *A. robustum*, having several cloacal systems in each colony — a character that readily distinguishes it from *A. marinense* and *A.*

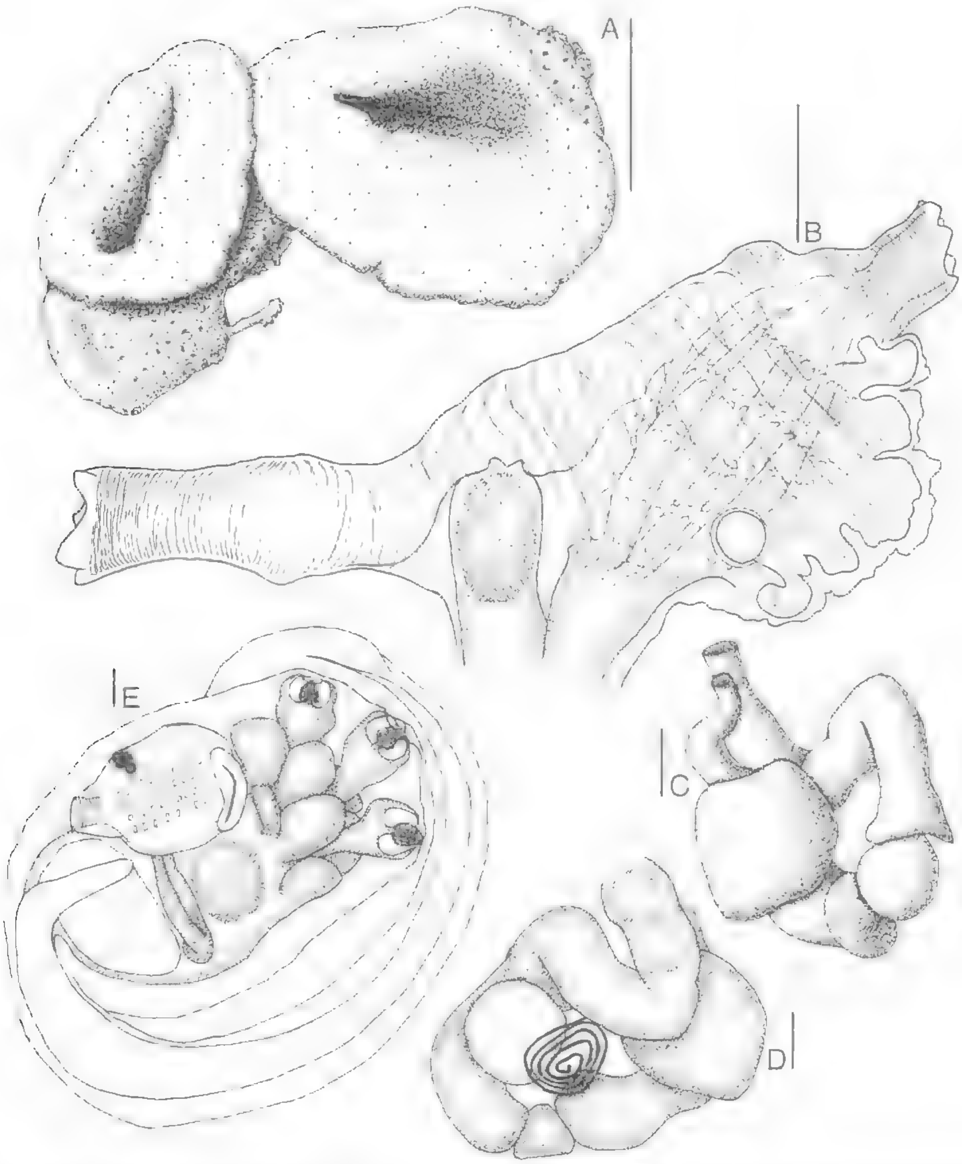


FIG. 7. *Atriolum lilium* sp. nov. (QM GH2385) – A, colony (from above) showing flaring apertures of shallow, open, common cloacal cavities; B, thorax; C, gut loop from right side showing elbow on rectum; D, gut loop from left side and gonads; E, larva. Scales. A, 1.0cm; B-E, 0.2mm.

eversum. *Atriolum robustum* has large cloacal apertures, but these do not flare out as in the present species. Further, *A. robustum* has much longer (to 5.0mm) zooids and lacks the large (0.1mm diameter) spicules. *Atriolum bucinum* has taller colonies that are opaque and bright red in life and its spicules have longer and more pointed rays.

Atriolum marinense sp. nov.
(Figs 8, 157E,F; Pl. 1C)

Atriolum robustum: Millar, 1988: 830; Monniot, 1989: 676; Monniot et al., 1991: 106.
? *Didemnum molle*: Bachmann et al., 1985: 1211 (part, specimens without symbionts from 40m).

TYPE LOCALITY. Coral Sea (Marion Reef, 8m, coll. N.Coleman 24.8.77 AMPI 208, syntypes QM G301616).

PREVIOUSLY RECORDED. Coral Sea (Chesterfield Reef – Monniot, 1989). New Caledonia (Monniot, 1989).

West Indian Ocean (Mozambique Channel – USNM 018451 Millar, 1988).

COLONY. Colonies are small (about 1cm high), firm, spherical to oval, upright flasks with a sessile apical cloacal aperture. Branchial apertures open about 0.5mm apart all around the outer surface. Short, stumpy attachment processes develop from a small area in the middle of the under surface. The colonies appear to subdivide as in *D. molle* (below), as one specimen in the syntype lot has 2 cloacal apertures on the upper surface and a slight vertical constriction around the colony, suggesting a subsequent division into 2 upright flasks. Another is two separate flasks with their adjacent surfaces joined to one another by narrow commissures of test. The other specimen is a single flask. Basically there is only a single system per colony in this species, more than one probably being an indication of imminent colony subdivision. The outer wall of the colonies are hard and firm, and the whole colony is relatively rigid. Usually, symbiotic plant cells are present on parts of the surface in what appears to be a non-obligate relationship.

Collector's notes (N. Coleman, 24.8.77) refer to the types as pink, although in photographs (AMPI 208) they appear to be cream (see also Monniot et al., 1991).

Spicules are in a thick, crowded layer in the surface. Another less crowded, thin layer of spicules lines the large, central cloacal cavity. Five-lobed atrial openings into the cloacal cavity are conspicuous, with 5 double rows of spicules outlining the lobes. The spicules are small, mostly up to 0.03mm in diameter although a few are as much as 0.04mm. They have 12 –15 long, club-shaped, pointed to blunt-tipped rays in optical transverse section, although some of the smaller ones have short conical rays. Some, when broken apart, are found to be hollow. They break up readily, and do not stay entire when attempts are made to prepare them for scanning electron microscopy.

ZOOIDS. These are 2 –3mm long, stretched between the branchial apertures on the outer surface and atrial apertures opening directly into the large internal cloacal cavity. The dorsum of the thorax extends out into the long atrial siphon. Thoraces are orange when first preserved but later lose their colour. Longitudinal muscles run the length of the thorax, the ventral ones from the branchial aperture. Others dorsal to them cross the dorsal mid-line and form a continuous series

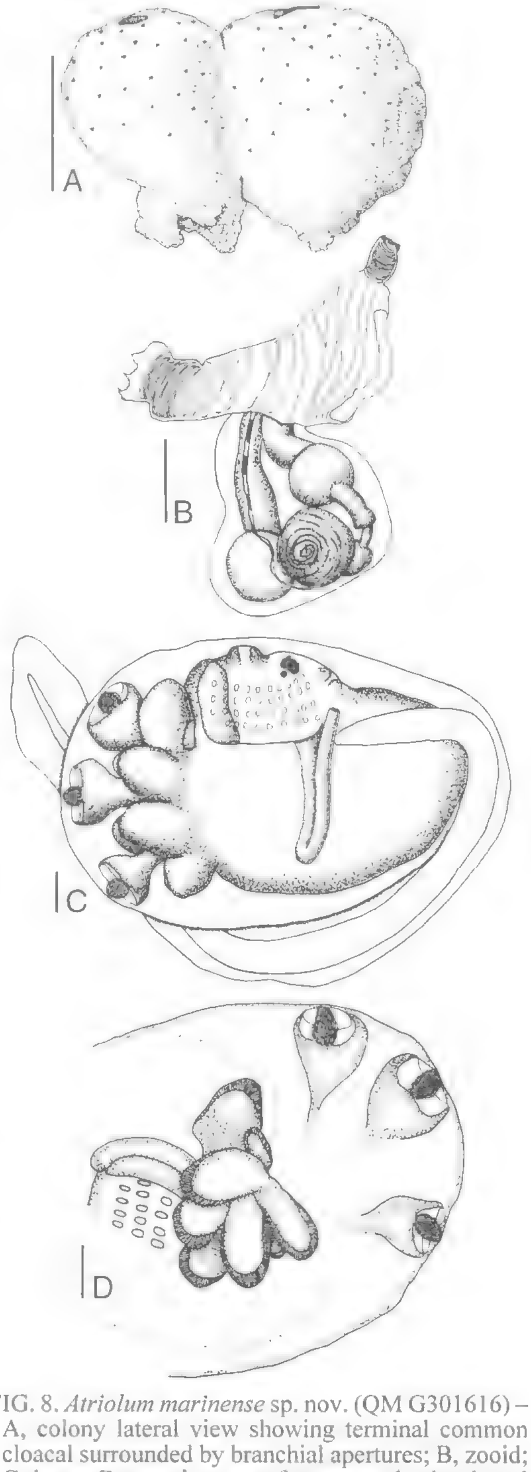


FIG. 8. *Atriolum marinense* sp. nov. (QM G301616) – A, colony lateral view showing terminal common cloacal surrounded by branchial apertures; B, zooid; C, larva; D, anterior part of metamorphosing larval trunk showing enlarged epidermal cells on the tip of each lateral ampulla. Scales: A, 5mm; B, 0.5mm; C,D, 0.1mm.

with the circular muscles on the atrial siphon. Sphincters are around the base of the branchial aperture and around the rim of the atrial aperture. Up to 20 oval stigmata may be in the anterior of the 4 rows of the branchial sac, but this could not be accurately determined because of the contracted thoraces. A deep lateral organ is half-way across the thorax, level with the last row of stigmata. When everted it has a narrow stalk.

A relatively short gut loop, has a thick duodenum constricted off from the oval posterior stomach; the gut increases in diameter abruptly (into a wide rectum) in the pole of the loop.

Mature male and female gonads are present together in zooids of the syntypes and embryos are being incubated in brood pouches. These separate from the zooids and lie free in the test when embryos become tailed larvae. The testis is undivided and has 7 coils of the vas deferens. The large ovum apparently moves up the oviduct to the thoracic brood pouch. Thoraces, abdomina and brood pouches all lie at the same level in the wall of the colony, the abdomen to the left and the brood pouch to the right of the dorsal mid-line of the thorax.

The larval trunk is about 1mm long. The 3 antero-median adhesive organs have long narrow stalks. Four ectodermal ampullae are on each side of the body, and a small accessory ampulla process projects forward from the top of the larval waist on the left. Four rows of about 12 stigmata are in the larval pharynx and a large otolith and ocellus in the cerebral vesicle.

REMARKS. This species is readily distinguished from *A. robustum* by its colony and smaller zooids (which are larger than those of *A. lilium*). The spicules are a similar size to those of *A. robustum*, but have fewer, longer and more rod-like rays with rounded tips, rather than the short conical rays of most other species of this genus. The only other species in which hollow spicules have been detected is *Polysyncraton circulum* (below).

Monniot (1989) reported symbiotic algae in this species. Although she did not indicate their location, it is most likely that they were on the outer surface as they are in the newly recorded colony. The rose colour of the New Caledonian specimens when first preserved apparently is the same as the pink recorded for the living syntypes.

Specimens from the Mozambique Channel assigned to *A. robustum* by Millar (1988) were reported to 'agree closely with Kott's account' (Millar, 1988: 8). This is true of the zooids, but re-examinaton of these specimens (USNM 018451) show the colonies to be the regular vase-shape of *A. marinense* rather than the massive, irregular colonies of *A. robustum*; and to have spicules characteristic of the former species — i.e. smaller than those of *A. robustum*. Monniot's (1989) contention that flask-shaped specimens from New Caledonia (of which she had photographs of living material) agreed well with Kott's (1983) description of *A. robustum* is even more difficult to understand. Indeed neither the description (Kott, 1983) of *A. robustum* nor the irregular type specimens are anything like the regular vase-shaped colonies of the present species, to which the New Caledonian material belongs.

Atriolum robustum Kott, 1983
(Figs 9, 157A; Pl. 1D)

Atriolum robustum Kott, 1983: 13, 1998: 80.
Not *Atriolum robustum*: Millar, 1988: 830. Monniot, 1989: 676. Monniot et al., 1991: 106 (< *A. marinense*).

NEW RECORDS. Queensland (Swain Reefs, QM G305675).

PREVIOUSLY RECORDED. Queensland (Swain Reefs – QM GH 1410 Kott, 1983; Raine I. – QM GH286 Kott, 1983). Torres Strait (Murray I – QM GH285 holotype Kott, 1983).

COLONY. The tough, irregular colony is tuber-shaped with short, tapering attachment processes projecting from its base. These probably support the colony off the substrate — they appear to be strong, rigid with pebbles attached at their narrow distal ends. Some large, rounded swellings up to 3cm diameter are along the upper surface, each with a central common cloacal aperture. Despite Kott's (1983) comment that these are numerous, there are only 2 in the holotype. They are more numerous in QM GH286. Common cloacal apertures are sessile, and of varying sizes, some large and half everted exposing some of the internal lining of the cavity to the exterior. The large cloacal cavity extends through the centre of the colony, expanding into large chambers beneath each cloacal aperture. In life, the colony is said to be firm and tough, but gelatinous, and greenish-grey with orange-vermilion zooids, but beige translucent in preservative. The surface is firm, and in long-preserved specimens the test glassy. It always is very tough. Spicules are present only in the surface layer (where they are moderately crowded only around the branchial apertures, which appear as white points in the surface of the colony) and in the layer lining the large, central common cloacal cavity (where they are only sparse). Branchial apertures open all

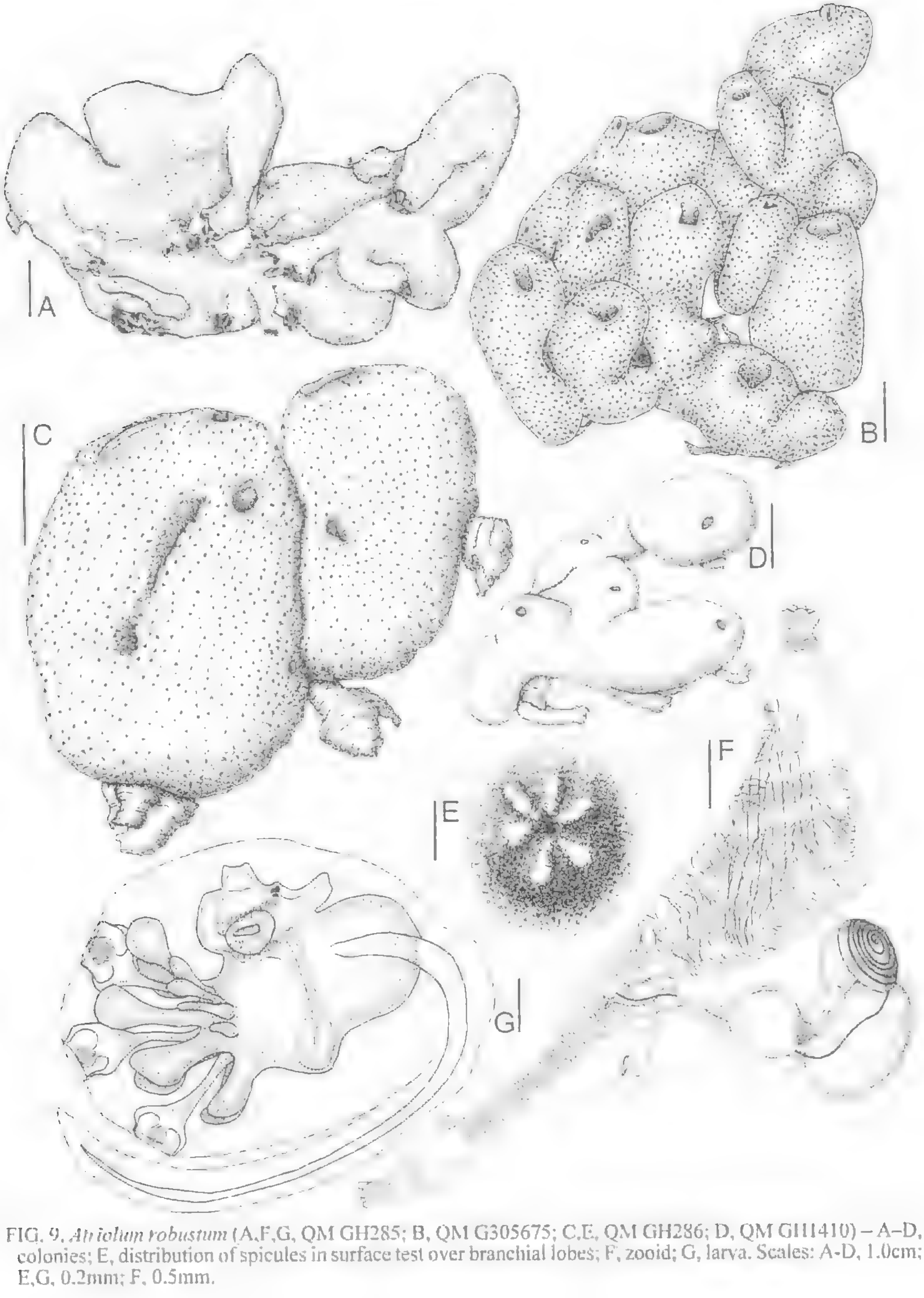


FIG. 9. *Atriolum robustum* (A,F,G, QM GH285; B, QM G305675; C,E, QM GH286; D, QM GH1410) – A–D, colonies; E, distribution of spicules in surface test over branchial lobes; F, zooid; G, larva. Scales: A-D, 1.0cm; E,G, 0.2mm; F, 0.5mm.

over the surface, even on the under surface between the attachment processes. Spicules also form white opaque points where they line the 5 lobes of the atrial apertures opening directly into the cloacal cavity. Spicules, up to 0.04mm in diameter are stellate with up to 18 short conical rays in optical transverse section. There is no conspicuous bladder cell layer in the surface test.

ZOOIDS. Zooids are the largest for any didemnid, being about 5mm long (thorax and abdomen together). The abdomen is bent up almost perpendicular to the longitudinal line of the thorax. The postero-dorsal part of the thorax is drawn out into a long atrial siphon, the line between the branchial and atrial apertures along the atrial siphon being almost a straight one stretched between the outer surface and cloacal cavity of colony. The thorax has the usual ventral longitudinal muscles extending from the branchial siphon to the posterior end of the thorax. More dorsal muscles extend across the dorsal border of the thorax and the base of the atrial siphon. Circular muscle bands along the length of the atrial siphon have branches that join them to adjacent bands and form a mesh along the length of the siphon. There are sphincters around the tip of the atrial siphon and along the length of the branchial siphon.

The dorsal ganglion is conspicuous. A curved neural duct opens directly into the pharynx. Pointed dorsal languets are on the transverse vessels, to the left of the dorsal mid-line. Stigmata are long, rectangular and up to 20 per row. A lateral organ is level with the centre of the last row of stigmata. A brood pouch is attached to the posterior side of the base of the atrial siphon by a narrow neck. The distal tip of the oviduct is diverted into this brood pouch where one ovum at a time appears to be fertilised and is incubated.

The gut loop has an almost spherical stomach, thick duodenum constricted off from an oval posterior stomach, and rectum expanding abruptly in the pole of the loop. The single undivided male follicle has the vas deferens coiled 6 times around its outer surface. The coiling is sometimes clockwise, sometimes anticlockwise, and sometimes the vas deferens loops back to change direction about halfway along its course.

Well developed larvae are in the holotype from Torres Strait and in the Raine I. specimen. These have a larval trunk about 1.2mm long. The 3 median adhesive organs have narrow stalks and shallow epidermal cups surrounding axillary cones constricted at their base. Nineteen stigmata are in the anterior of the 4 rows, and 16 are in the last. A large circular lateral organ is invaginated into the parietal body wall on each side of the larval pharynx. A large ocellus and an otolith are in the cerebral vesicle. Four ectodermal ampullae are along each side of the 3 antero-median adhesive organs and, on the left, 3 or 4 small accessory ampullae are in a vertical row projecting forwards from the larval waist at the base of the primary ones.

REMARKS. The small spicules are more or less the same size as those of *A. marinense* but have conical rather than club-shaped rays. They are similar to, but smaller than those of *A. lilium* and *A. tubiporum* and with more rays. This species is distinguished by having larger colonies, zooids and larvae than other known species. It resembles *A. lilium* in its large and irregular colonies with several cloacal systems. However, although its cloacal apertures often are wide they do not expose the whole of the cloacal cavity as they do in *A. lilium*.

The large lateral organ in the larval thorax is an unusual feature, shared only with *Didemnum fucatum*. Vanadium at 350ppm was contained in a small sample of QM G305675.

Atriolum tubiporum sp. nov.
(Figs 10, 157C; Pl. 1E)

Askonides coelenteratus Kott, 1962:292 (part, specimen from Green Pools)

TYPE LOCALITY. Western Australia (Albany Harbour, bay at western end of Breaksea I. Albany, 20m, coll. AIMS Bioactivity Group Q66C-2858 25.3.89, holotype QM G302885).

FURTHER RECORDS. Western Australia (off Dongara, 29°50'S, 114°24'E, 128-130m, coll. CSIRO Cruise DM6, statn 214, 11.10.63 QM G302293); Green Pools, AMY1346 Kott, 1962.

COLONY. Colonies are firm, thick tubes or cylinders to about 1cm diameter and 1cm long from thick, sometimes branched basal stalks up to 2cm or more long. Cloacal apertures are terminal, regular and circular, in the centre of the free end of each cylinder. Occasional cloacal apertures, probably from newly developing systems are at the base of the lobes, or on the common stalks. Photographs show that in life the cloacal apertures expand to the full diameter of each cylinder so that it is open at the top. Branchial apertures which appear as dimples in preserved material are evenly distributed over the outer surface of the colony and have spicules in the siphonal lining. The atrial openings into the

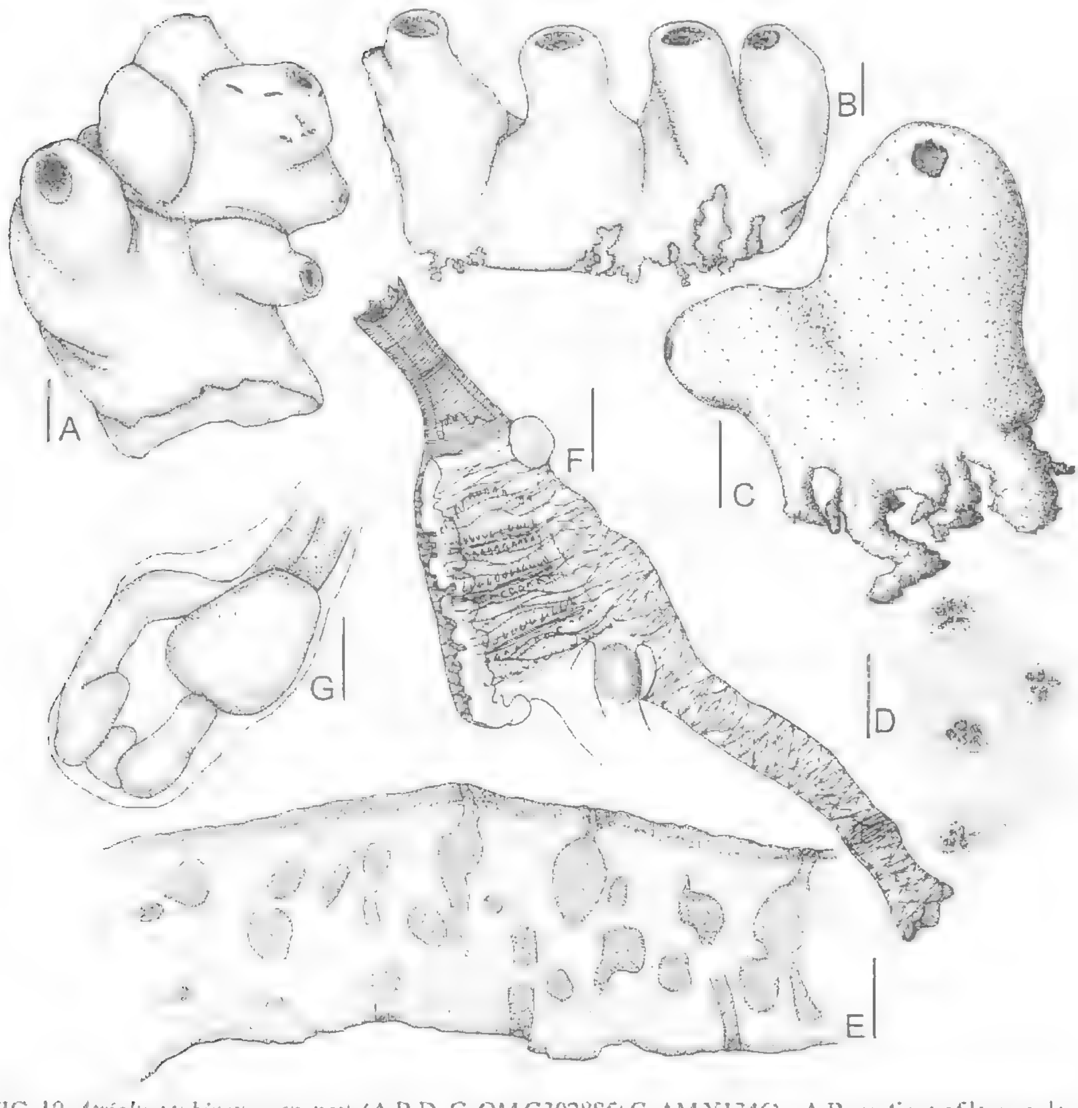


FIG. 10. *Atriolum tubiporum* sp. nov. (A,B,D–G, QM G302885; C, AM Y1346) – A,B, portions of large colony; C, small colony; D, spicules in siphon linings seen from the surface; E, semidiagrammatic section through the colony wall cutting through zooids stretched between external and internal surfaces, the branchial apertures on the outer surface and atrial apertures in the central cloacal cavity; F, thorax showing long atrial siphon; G, gut loop. Scales: A–C, 5.0mm; D, 0.5mm; E, 1.0mm; F,G, 0.2mm.

central cloacal cavity are conspicuous, having 5 clumps of spicules in each siphonal lining.

Spicules are evenly distributed in a thin layer in the surface and in the test lining the cloacal cavity, and are relatively sparse throughout the remainder of the test. They are stellate to 0.08mm diameter mostly with about 11 short conical rays in optical transverse section. Also, occasional spicules have about 7–9 more pronounced and acutely pointed rays. The colour of living specimens is white and cream; but they are cream in preservative.

ZOOIDS. Zooids are large, to 3mm between branchial and posteriorly oriented atrial aperture. Abdomina are bent ventrally from the long axis that passes through the branchial siphon, pharynx and atrial siphon between the outer surface of the colony to the central cloacal cavity. The rim of the branchial aperture is divided into 6 lobes, and 5 small pointed projections are around the rim of

the atrial aperture. The atrial siphon is about twice the length of the abdomen, and is surrounded by circular muscles that branch and anastomose with one another along its length. Longitudinal muscles extend along the thorax, and transverse muscles are in both the parietal body wall and the interstigmatal transverse bars. Thoraces are roomy, with perhaps 12 long stigmata (rounded at each end) per row, but these were hard to count owing to contraction. There are large (about 0.089mm diameter) plate-like lateral organs each side of the thorax, about opposite the third row of stigmata. Abdomina are relatively short, half their length occupied by the oesophageal neck. The simple, straight gut loop has a rounded stomach, and short rounded post-pyloric loop. The oviduct is expanded at the top of the oesophageal neck, but in these specimens there is no developed brood pouch, nor are the gonads developed.

REMARKS. Although gonads are not present, these colonies have been assigned to *Atriolum* rather than *Leptoclinides* on the basis of their large central common cloacal cavities, large, circular common cloacal apertures that resemble those of *A. marinense*, long muscular atrial siphons, and large zooids with transverse muscles in the body wall. The species resembles *A. robustum*, but it has larger spicules with fewer rays and narrow tube-like cylindrical lobes. The species also resembles *Leptoclinides coelenteratus* which has less regularly cylindrical colony lobes, shallower common cloacal cavities not confined to primary central cavities, shorter atrial siphons; and smaller spicules with more acutely pointed rays.

Spicules of the specimen from off Dongara (Western Australia), preserved in neutralised formalin, were soft but distinguishable and were found concentrated around the zooid openings when first examined in 1976. Although transferred out of formalin at that time, the spicules had disappeared altogether when this specimen was re-examined in 1993. The colony is flask-shaped, and the test is firm and gelatinous.

Leptoclinides marsupialis (Monniot, 1989) is also similar to the present species but lacks the generic characters of *Atriolum* — it does not have the long posteriorly directed atrial siphon, and its common cloacal system is not confined to the single central chamber of the present species. Further, its test is brittle and packed with spicules.

Genus **Leptoclinides** Bjerkan, 1905

TYPE SPECIES. *Leptoclinides faroensis* Bjerkan, 1905.

The genus has large, robust colonies with generally large posterior abdominal cloacal chambers, relatively large zooids, posteriorly oriented atrial apertures on relatively long siphons, conspicuous parallel longitudinal (but rarely transverse) muscles in the parietal body wall, coiled vas deferens, and large larvae usually incubated in the basal layer of test. Dorsal pharyngeal muscles are particularly delicate consisting of 3–4 fibres, longitudinal parietal bands terminate at the posterior end of the thorax (rather than joining the dorsal pharyngeal muscle bands ventral to the oesophagus to form a retractor muscle). In most species, zooids are not readily removed from the test. Columnar ectodermal cells have been detected projecting from the body wall in relatively few species. Branchial lobes often are not developed and when present are invariably short. The rim of the atrial aperture often has 5 small pointed projections around it. The atrial sphincter usually is short and confined to the distal part of the siphon. Most species have large, stellate spicules with conical rays sometimes pointed, but often chisel-shaped or with a truncated flattened tip. Burr-shaped and globular spicules also occur. A large lateral organ is on each side of the thorax near the posterior end of the branchial sac (on each side of the base of the atrial siphon). The short gut loop in *Leptoclinides* has a smooth pear-shaped stomach, a thick and long duodenum, a short oval posterior stomach, and a wide rectum that expands abruptly from a constriction at the distal end of the posterior stomach in the pole of the gut loop. The rectum constitutes the whole of the ascending limb of the gut loop and has a constriction surrounded by tubules of the gastro-intestinal gland halfway up. Testis follicles usually are numerous, but in a few species (including the type) the testis is undivided. Larvae are relatively large (sometimes more than 1.0mm), and usually have 2–4 lateral ampullae per side, although occasionally there are 6–8. The oozooid has 4 rows of stigmata and generally the adult organs are well advanced. Larval blastozooids do not occur.

Leptoclinides spp. have been found to contain large amounts of vanadium, an element which, apart from a small amount detected in *Atriolum robustum*, has not been detected in other genera of this family (Hawkins et al., 1983). Its presence suggests a primitive phylogenetic position. It is

assumed here that the multiplicity of male follicles also indicates an ancestral position for this genus, as does the relatively large size of the zooids and the presence of an atrial siphon.

Leptoclinides is readily distinguished from most other genera of the family by a combination of characters rather than any one character. The chisel-shaped tips of spicule-rays found in many species of this genus occur only occasionally in other genera. *Atriolum* has larger zooids, larger atrial siphons with strong circular muscles along their whole length, transverse muscles in the parietal body wall, and colonies with a large uninterrupted central cloacal cavity surrounded by a single layer of test containing zooids and embryos, rather than the extensive 3-dimensional spaces of *Leptoclinides*. With the exception of the large uninterrupted cloacal cavity beneath the cloacal apertures, the common cloacal cavity in *Leptoclinides* is interrupted by connectives between basal and surface layers of test and the zooids are in the surface, while embryos are incubated in the basal test.

Trididemnum resembles *Leptoclinides* in often (but not always) having a posteriorly oriented atrial siphon and posterior abdominal cloacal cavity, and often (but not always) large larvae, with only 3 or 4 long ampullae per side, a pronounced waist between the adhesive array and the rest of the larval trunk and usually lacks larval blastozooids. However, its zooids are smaller than in *Leptoclinides*, with a retractor muscle, and only 3 rows of stigmata in adult zooids and oozooids.

Included here as a synonym of *Leptoclinides*, is *Askonides* Kott, 1962. The genus was distinguished by the large cloacal chambers into which zooids opened directly, and the 5 lobes on the rim of each atrial aperture. Both those characters are present in *Leptoclinides* sometimes, and in *Atriolum* always. In *Leptoclinides* the absence of the atrial lobes appears to be associated with a reduction in zooid size but, often they have been overlooked, sometimes because they are small, and sometimes because siphons are difficult to remove entire from the test. The very large cloacal chambers with zooids opening directly into them in species formerly assigned to *Askonides* appear to be homologues of the large terminal chambers that are part of the three dimensional systems of *Leptoclinides* spp. rather than homologues of the large central cavity of *Atriolum*.

Coelocormus huxleyi Herdman, 1886, known from a single specimen taken off the coast of Patagonia, also shares some characters with *Leptoclinides*,although it is not impossible that it is a species of *Atriolum*. It is a vase-shaped colony, about 3cm long, which Herdman thought to have been unattached. He reports a cloacal aperture in the base of the central cavity of the vase, with 5-lobed branchial apertures opening around the inside lining of the cavity. These actually may be atrial apertures, which are characteristically 5-lobed in all *Atriolum* and many *Leptoclinides*. Herdman's (1886, pl. 37, fig. 3) section through the colony (vase) wall, showing zooids stretched between the outside and inner surfaces tends to support the view that it is a species of *Atriolum*. As in *Atriolum*, there do not appear to be any secondary cavities. However, in *C. huxleyi* the vas deferens coils around several pyriform male follicles, and large tailed embryos are being incubated in the basal test which suggests *Leptoclinides* (similar to *L. coelenteratus*) rather than *Atriolum*.

Leptoclinides glauerti Michaelsen, 1930, from Shark Bay, Western Australia, is said to lack a cloacal cavity, the atrial apertures opening through the base of the colony, and the branchial apertures on the upper surface. The dorsal border of the thorax is stretched between the upper and lower surfaces of the colony. Michaelsen's (1930) speculative evolutionary pathway to this colony form involves the opening up of the cloacal cavity to the exterior. Indeed, this appears to have occurred in *Atriolum lilium*, and in *A. eversum* the whole colony appears to have turned inside out with the atrial apertures on the outside and the branchial apertures in the concavity of the cup. It is possible that *L. glauerti* represents a stage in the evolution of the colony that is more or less equivalent to the *A. lilium* condition. In *L. glauerti* a thick bladder cell layer is on both the branchial and atrial surfaces of the colony, spicules are in the middle layer of test. They are 0.045mm in diameter, and have 9 or 10 rays in optical section. There is a plate-like lateral organ each side of the base of the atrial siphon. A problem in Michaelsen's interpretation of the colony is how it could be fixed to the substrate, since each surface is interrupted either by incurrent or excurrent apertures of zooids. It is not impossible that the type specimen is only the upper portion of a colony with the base (below the cloacal cavity) missing. There was no sign of gonads in Michaelsen's colony and it cannot be positively assigned to either *Atriolum* or

Leptoclinides. However, the atrial siphons are not as long as in *Atriolum* and probably it is a *Leptoclinides* sp. Its most likely affinity is with *L. rufus* which has similar bladder cell layers and spicules.

Determination of species in this genus has been as confused and confusing as in other didemnid genera. Zooids are relatively uniform and do not provide many characters by which species can be distinguished. Too much reliance has been placed on the colour and shape of pigment cells (which are variable, and often lost or altered in preservative). Reliable characters are found in the shape, size and distribution of the spicules, course of the gut, number and arrangement of testis follicles, number of vas deferens coils, form of the branchial siphon, and structure of the cloacal systems.

Species occurring in Australia are conveniently divided into at least 6 groups. However only the *dubius* and *brandi* groups can be confidently regarded as monophyletic. These groups are:

1. The *dubius* species group, characterised by the absence of a distinct spicule-free superficial bladder cell layer, small (not more than 0.04mm diameter) spicules of several types which usually form a layer in the surface of the colony (but sometimes are present throughout) and project in to line the branchial siphons and outline the margins of the distinctly stellate apertures, a small circular lateral organ, usually a wide velum in the base of the branchial siphon which projects up to form a short cylindrical secondary siphon (absent in *L. durus*) with 6 small lobes around the rim and strong circular muscles, a long gut loop with its distal part bent up ventrally against the proximal part to form a double loop, 9 or more testis follicles in a spherical 3-dimensional mass, the proximal end of the vas deferens coiled only twice or following an S-shaped course, and the ovary producing a single egg at a time, on the outside of the testis over the proximal end of the vas deferens (at the posterior end of the zooid). Known larvae are large — the larval trunk 1mm long or more, and they have 4 or more pairs of lateral ampullae.

Members of this group are *L. dubius*, *L. kingi*, *L. multilobatus*, *L. durus*, *L. echinus* and *L. levitatus*.

2. The *coelenteratus* group sometimes has a thin superficial layer of bladder cells through which the branchial siphons of the zooids, surrounded by spicules, penetrate to reach the surface. Spicules and/or pigment cells often are found in the bladder cell layer. In *L. apertus* and *L. cuspidatus* spicules are crowded at the surface and there is no apparent bladder cell layer superficially. Spicules are relatively large (up to 0.08mm or more in diameter) the majority with short, conical rays. They do not outline stellate branchial apertures as they do in the *dubius* group although they usually form a plug inside the siphons when the zooids are contracted. The lateral organs are large and plate-like. The rim of the atrial siphon usually has 5 lobes or papillae on it and 5 rows of spicules mark these openings into the common cloacal cavities. The common cloacal systems are dominated by large, central chambers beneath the terminal cloacal apertures. Also, around their margins, the central cavities are continuous with large horizontal posterior abdominal chambers interrupted by test connectives anchoring the surface zooid-bearing test to the basal test. Testis follicles (3–8) are in one plane, in a circle or ring at the side of the distal end of the straight gut loop, which is either vertical or the whole loop is bent ventrally, at right angles to the thorax. The vas deferens coils at least 4 times. Usually species in this group have a long larval trunk (1.1mm), and the number of ectodermal ampullae is never more than 4 per side.

Included in the group are *L. apertus*, *L. coelenteratus*, *L. cavernosus*, *L. imperfectus* and *L. cuspidatus*.

3. The *rufus* group is characterised by its relatively smooth, and often flat surface, with a conspicuous superficial layer of bladder cells, usually mixed with pigment cells. Maximum sized spicules are 0.04–0.08mm diameter with 7–9 conical rays. Four to 6 male follicles are arranged in a circle, converging to the vas deferens which makes from 5–7 coils. Larvae have 2–4 pairs of lateral ampullae and the trunk is only about 0.6mm long. *L. rufus*, *L. placidus* and *L. variegatus* are flat, the cloacal system dominated by horizontal spaces; while in *L. longicollis* and *L. compactus* the colony has protuberant lobes on the surface, formed by thickening of the basal layer of test to form a central core. The central core of test is surrounded by cloacal spaces separating it from the outer layer of zooid-containg test. This peripheral sub-surface cloacal space is homologous with the posterior abdominal horizontal spaces, and is crossed by test connectives.

4. The *lissus* group may be polyphyletic. Only two species are assigned to it, *L. lissus* and *L. maculatus*. Both are flat, without a superficial layer of bladder cells, and with a horizontal cloacal cavity and relatively small stellate spicules.

5. The *volvus* group has cloacal canals lined on each side with a row of zooids. The surface test is depressed over the canals, which surround zooid-free areas of test that protrude from the surface of the colony. The group may not be monophyletic, as it contains the stalked species *L. comitus* and *L. volvus* with some globular spicules, as well as the sheet-like *L. rigidus* and *L. exiguus* with stellate spicules to 0.07mm diameter.

6. The *brandi* group has some of the characters of the *coelenteratus* group, viz. large cloacal cavities, testis follicles in a single plane and large spicules. However, the regularly stellate spicules, with fewer, longer and more pointed conical rays are in a layer at the surface, and there is no superficial layer of bladder cells. The group may be closer to *Atriolum* than others, having a longer atrial siphon and a brood pouch. The larva of *L. marsupialis* resembles that of the *coelenteratus* group, with only 2 ectodermal ampullae per side and a relatively small trunk — less than 0.6mm long. *L. brandi* has up to 8 lateral ampullae (like larvae of certain members of the *dubius* group) in a larva of 0.75mm trunk length. Members of this group are *L. brandi* sp. nov. and *L. marsupialis* Monniot, 1989.

Leptoclinides fungiformis with a horizontal cloacal cavity beneath the surface zooid-bearing layer of the colony, is distinguished from the *rufus* group by its unusually small, globular spicules.

Leptoclinides is known from only one species in the northern Atlantic (Van Name 1945) and only 2 from the tropical Atlantic (Monniot, 1983). It does not occur at all in the seas around the British Isles, and is not known in the southern temperate Atlantic, the Mediterranean or the eastern Pacific. It does not occur in Antarctic waters, and is known from only one species in the Subantarctic (Kott, 1969). However, it is well represented in the western Pacific – New Caledonia (Monniot, 1989), Indonesia and the Palau Is (Sluiter, 1909; Monniot & Monniot, 1996), around the Australian continent (where a number of robust tropical species as well as temperate ones occur), New Zealand (Millar, 1982) and Japan (Tokioka, 1953).

KEY TO SPECIES OF *LEPTOCLINIDES* RECORDED FROM AUSTRALIAN WATERS

1. Testis a 3-dimensional mass; post-pyloric part of gut loop bent up to form a secondary loop; usually a false siphon at base of branchial siphon (*dubius* group). 2
   Testis not a 3-dimensional mass; post-pyloric part of gut loop not bent up to form a secondary loop; false siphon not present at base of branchial siphon. 7
2. Spicules crowded throughout the test; no false siphon . . . . *L. durus* sp. nov.
   Spicules not crowded throughout the test; false siphon present 3
3. Spicules generally more than 0.03mm 4
   Spicules generally not more than 0.02mm diameter . . . . *L. multilobatus*
4. Spicules globular and stellate; 13 or more rays in optical transverse section 5
   Spicules only stellate; 9-11 rays in optical transverse section. . . . . *L. echinus* sp. nov.
5. Stellate spicules some with conical, others with fusiform rays 6
   Stellate spicules with conical rays only . . . . . *L. kingi*
6. Stellate spicules with, 13-15 rays in optical transverse section . . . . *L. levitatus* sp. nov.
   Stellate spiculres with up to 17 rays in optical transverse section . . . . *L. dubius*
7. Colony stalked 8
   Colony not stalked 9
8. Zooids arranged in double rows around zooid-free areas of test; common cloacal cavities are oesophageal canals . . . .*L. volvus*
   Zooids not arranged in double rows around zooid-free areas of test; common cloacal cavities are posterior abdominal spaces . . . . *L. fungiformis*
9. Spicules mostly globular . . . . *L. comitus* sp. nov.
   Spicules mostly or all stellate 10
10. Spicules with more than 15 rays in optical transverse section . . . . *L. carduus* sp. nov.
    Spicules with no more than 15 rays in optical transverse section 11
11. Spicules evenly distributed throughout the colony . . 27
    Spicules not evenly distributed throughout the colony .12
12. Superficial bladder cell layer conspicuously thick, always without spicules in it 13
    Superficial bladder cell layer not conspicuously thick, often with some spicules in it, or absent altogether . . 14
13. Spicule rays set in concave base in central mass . . . . *L. umbrosus* sp. nov.
    Spicule rays not set in concave base in central mass . . . . *L. rufus*
14. Spicules with chisel-shaped tips present 15
    Spicules with chisel-shaped tips not present 26
15. Common cloacal apertures terminal on conspicuous conical or rounded elevations 16
    Common cloacal apertures not terminal, and no conspicuous surface elevations 19
16. Stigmata 14 – 16 per row . . . . *L. cuspidatus*
    Stigmata less than 14 per row 17
17. Spicules with truncated rays present . . . .*L. imperfectus*
    Spicules with truncated rays not present 18

18. Spicules with 7 – 9 rays in optical transverse section; tropical species . . . . *L. sulawesii*
Spicules with 9 – 11 rays in optical transverse section; temperate species . . . . . . *L. compactus* sp. nov.
19. Spicules with 13 – 15 rays in optical transverse section, to 0.15mm diameter . . . . *L. erinaceus* sp. nov.
Spicules with not more than 13 rays in optical transverse section, not more than 0.1mm diameter 20
20. Surface test conspicuously depressed over deep, circular, primary common cloacal canals 21
Surface test not conspicuously depressed over deep circular primary canals . . . . *L. variegatus* sp. nov.
21. Common cloacal cavities include posterior abdominal components 22
Common cloacal cavities never posterior abdominal . 25
22. Vas deferens coils 8 times around testis . . . . *L. maculatus* sp. nov.
Vas deferens coils 5 or 6 times around testis 23
23. Spicule ray-tips sometimes truncated . . . . *L. constellatus* sp. nov.
Spicule ray-tips never truncated 24
24. Stigmata up to 10 per row; temperate species . . . . *L. exiguus* sp. nov.
Stigmata more than 10 per row; tropical species . . . . *L. rigidus* sp. nov.
25. Spicules to 0.096mm diameter . . . *L. aciculus* sp. nov.
Spicules to 0.06mm diameter . . . *L. seminudus* sp. nov.
26. Stigmata fusiform; brood pouch present; spicule rays long, attenuated; colony not narrow vertical lobes . . . . *L. brandi* sp. nov.
Stigmata not fusiform; brood pouch not present; spicule rays not long, attenuated; colony narrow vertical lobes . . . . *L. longicollis* sp. nov.
27. Spicules to 0.2mm diameter or more. . . . . *L. magnistellus* sp. nov.
Spicules less than 0.2mm diameter 28
28. Spicules with chisel-shaped ray tips . . . 29
Spicules without chisel-shaped ray tips 31
29. Colony sheet-like; no large surface prominences with terminal cloacal apertures; spicules with 9 – 13 rays in optical transverse section 30
Colony not sheet-like; large surface prominences or upright lobes with terminal cloacal apertures present; spicules with 13 – 15 rays in optical transverse section . . . . *L. cavernosus* sp. nov.
30. Dark pigment in superficial bladder cell layer . . . . *L. albamaculatus* sp. nov.
Dark pigment not in superficial bladder cell layer . . . . *L. placidus* sp. nov.
31. Common cloacal system with an uninterrupted central chamber . . . . *L. coelenteratus*
Common cloacal system lacks an uninterrupted central chamber 32
32. Bladder cell layer present superficially 33
Bladder cell layer not present superficially . . . *L. lissus*
33. Spicule rays 7 – 9 in optical transverse section . . . . *L. caelestis* sp. nov.
Spicule rays 13 – 15 in optical transverse section . . . . *L. confirmatus* sp. nov.

Other species of *Leptoclinides* found in adjacent areas are:

Leptoclinides apertus Monniot, 1989 from New Caledonia is known from a range of colonies of diverse colour and form — yellow orange to, rust to black investing sheets to upright lobes. Zooids have a wide open atrial aperture that may have been caused by over narcotisation. The vertical gut loop only slightly flexed at the pole resembles that of *L. cuspidatus* (Sluiter, 1909) as do the spicules. Both species have a similar range in colony form. The New Caledonian species has more numerous vas deferens coils but a smaller larva. *Leptoclinides marsupialis* (Monniot, 1989) also is similar to *L. apertus* but differs in its fusiform stigmata and its brood pouch, and is more like *L. brandi*.

Leptoclinides dobocnsis (Sluiter, 1913) from Aru Is was reported by Sluiter (1913) to have a large atrial lip, and was assigned to *Polysyncraton*. However, its holotype (SM411) was re-examined by Monniot (1989) and assigned to *Leptoclinides*. Re-examination of the type in the present study has confirmed Monniot's generic assignment. The species resembles *L. placidus* in having a thin superficial layer of bladder cells, and a similar cloacal system. The zooids are relatively small with 8 stigmata in the first 2 rows and 6 in the last row, a short posteriorly oriented atrial siphon, and 6 coils of the vas deferens around 4–5 male follicles. A few larvae are in the basal test.

Leptoclinides hawaiiensis Tokioka, 1967 has massive upright or investing colonies with large posterior abdominal cavities. Thickened basal test forms a central mass in the upright colonies. Spicules, found in only one colony, are posterior to the abdominal layer of test, and are more than 0.1mm in diameter.

Leptoclinides madara Tokioka, 1953 from Japan, resembles *L. rufus* in the form and distribution of spicules and bladder cells, although its atrial siphons are larger and pigment cells larger and more ribbon-like. Although Kott (1981) proposed *L. rufus*: Eldredge, 1967 as a synonym of *L. madara*, Eldredge's material may include more than one species, including *L. rufus* (tan with orange streaks) and a Hawaiian species without a bladder cell layer. Kott (1981) also proposed *L. marmoratus*: Millar, 1975 as a synonym of *L. madara*, but it appears to be conspecific with *L. rufus*, having similar colony, zooids and larvae.

Leptoclinides marmoratus (Sluiter, 1909) from Indonesia always has a superficial layer of bladder cells, and a spicule-free area over the anterior end of each zooid, with 3 clumps of spicules in the centre of each aperture (in the siphon lining). Spicules are also in cloud-like patches in the test around and between the zooids, but elsewhere the internal test is free of spicules and is spongy. The spicules (to 0.03mm diameter) are distinctive with many long, rod-like, blunt-ended or pointed rays. Common cloacal cavities are beneath the large terminal cloacal apertures on surface prominences, and posterior abdominal canals open into these cavities. Atrial apertures are on short posteriorly directed siphons. About 12 stigmata are in the middle rows. The vas deferens coils 6 times around a clump of about 7 male follicles crowded into a circle in a single plane. The

whole of the gut loop (including the stomach) sometimes is bent up at right angles to the longitudinal axis of the thorax.

The species is distinguished from *L. rufus* and *L. cavernosus* (both of which have a superficial layer of bladder cells and clumps of spicules in the siphon lining) by its unique small, globular and burr-like spicules with narrow, cylindrical and fusiform rays, and by the discontinuity in the layer of spicules beneath the bladder cell layer.

Specimens of *L. marmoratus* examined are the lectotype (part ZMA TU837.1), ZMA TU837.2, a colony (ZMA TU475.3) formerly assigned to *Didemnum reticulatum* Sluiter, 1909, and all specimens of *Polysyncraton ocellatum* (below). The specimens of *P. ocellatum*, and most *L. marmoratus*, are from Siboga Station 64. The exceptions are the specimen from Station 312 (ZMA TU837.2) from 274m and the one from Station 53 (ZMA TU475.3). USNM 5899 from the Philippines, doubtfully assigned to *Polysyncraton dubium* by Van Name (1918: Station D5109), has similar spicules to *L. marmoratus* but on re-examination has been found to be *Lissoclinum patella*.

Millar (1975) believed that *L. marmoratus* was a junior synonym of *L. reticulatus*: Hastings, 1931 (<*L. rufus*, see below), but re-examination of its syntypes has shown that this is not so. *Leptoclinides ocellatus*: Tokioka, 1953 from Japan is not a synonym of *L. marmoratus*, having very different spicules.

Small globular and burr-like spicules are unusual in this genus, being more often encountered in *Polysyncraton*, *Didemnum* and *Lissoclinum*.

Leptoclinides marsupialis (Monniot, 1989) from New Caledonia, originally assigned to *Atriolum*, has spicules, gonads, and brood pouch like *L. brandi* from which it is distinguished by its yellow-orange to black pigment and thin brittle colonies with spicules throughout the test (see also *L. apertus* Monniot, 1989).

Leptoclinides multipapillatus Monniot, 1989 from New Caledonia has 5–7 male follicles with 5 coils of the vas deferens. Several eggs are at different stages of maturity in the ovary. The species is named for the large number of larval ampullae (about 10 per side). The cloacal system is not described. The species is distinguished by its black colony, large zooids and numerous larval ampullae. It apparently has regularly stellate spicules (with about 7 conical pointed rays in optical section) to at least 0.04mm diameter, although Monniot (1989) has not recorded the full size range of the spicules. Spicules are concentrated in the surface and are sparse elsewhere.

Leptoclinides namei Michaelsen, 1930 is a name conferred on 2 Philippine specimens, each with 4 vas deferens coils, included in *Polysyncraton dubium*: Van Name, 1918 (D5555, D5139 – USNM 5996, 6033 respectively). The name must be considered a *nomen nudum*, as the statement merely that it is not conspecific with another does not constitute a species description. Van Name (1918) himself was not confident that these specimens were conspecific. The specimen USNM 5996 (see *Polysyncraton dubium*: Van Name, 1918) has not been located; and USNM 6033 is discussed below (*Leptoclinides dubius*, Remarks).

Leptoclinides ocellatus (Sluiter, 1909) from Indonesia (lectotype ZMA TU839 and paralectotype ZMA TU1276) are junior synonyms of *L. marmoratus* (Sluiter, 1909). In specimens Sluiter assigned to *P. ocellatum*, the spicules are in a wide collar-like band around each branchial aperture and are generally more regularly arranged than in *L. marmoratus*, in which they spread out in the surface test around each zooid. This does not constitute a specific difference, since the distribution of the spicules around the branchial apertures displays some intraspecific variation.

Leptoclinides quadratum (Monniot & Monniot, 1996) From Chuuk Atoll, was described in *Atriolum*. It has 2 or 3 testis follicles, 4 coils of the vas deferens, a brood pouch and vertical lobes with terminal common cloacal apertures. The thorax and abdomen together is smaller than the zooids of *Atriolum* (zooids are not more than 1.5mm long — assuming that the thorax of the figured specimen is contracted to half its usual length, while zooids of *Atriolum* are 3–6mm). The atrial siphon is significantly shorter and lacks the 5 atrial lobes invariably present in *Atriolum*. The thoracic musculature is said to be weak, the conspicuous circular muscles and the transverse thoracic siphonal muscles of *Atriolum* apparently not being present. Unfortunately the cloacal systems are not described. The species appears to belong to *Leptoclinides*. Its spicules are the same size and form as those of *L. brandi*, which also has a brood pouch. However, *L. brandi* has 5 rather than 4 coils of the vas deferens, characteristic long fusiform stigmata pointed at both ends, and sheet-like colonies lacking the parallel vertical lobes of the present species.

Leptoclinides robiginis Monniot, 1989 from New Caledonia has extensive encrusting colonies with spicules irregularly concentrated in the superficial layer of test. Cloacal cavities are shallow, restricted and presumably at oesophageal level (they are reported as not being very deep in the colony). The atrial aperture is open, sessile and directed laterally. There are 3–6 loose male follicles and vas deferens coils, spicules stellate and not more than 0.025mm diameter, with about 9–11 conical rays in optical section (Monniot, 1989: pl. 1F), a large cylindrical larval trunk with a ring of ampullae, and red coloured living colonies. Monniot (1989) recorded zooids with a wide open atrial aperture and bidentate anterior lip which with the loose vas deferens coils and testis follicles may indicate *Polysyncraton*.

Leptoclinides uniorbis Monniot & Monniot, 1996 from Micronesica, has a hard colony and stigmata, testis follicles and vas deferens like *L. durus*. It is distinguished only by its spicules with more numerous and sometimes long rod-like rays.

Undescribed species of *Leptoclinides* are:

Polysyncraton dubium: Van Name, 1918 (part, D5139, USNM 6033 from the Phillipines) has about 10 male follicles in a 3-dimensional mass, but differs from *L. dubius* in its surface layer of bladder cells, 6 coils of the vas deferens and straight gut loop. This is one of the specimens assigned to *Leptoclinides namei* Michaelsen, 1930.

Leptoclinides sp. WAM 569.89 from Cocos Keeling I., has, like species of the *dubius* group, a layer of spicules lining the branchial siphons, only one coil of the vas deferens and it lacks a superficial bladder cell layer. However, it lacks the spherical mass of male follicles of that group, having only 5 male follicles in a single plane — 4 in a ring around the outside, and one in the centre. The spicules resemble those of *L. marmoratus*, being spherical with numerous, fine rays, but *L. marmoratus* has more numerous coils of the vas deferens.

Leptoclinides reticulatus: Tokioka, 1967, (part) from Kiribati (USNM 11492) is a large, upright, aspicular colony with a terminal cloacal aperture. It appears to be an undescribed species.

Leptoclinides reticulatus: Tokioka, 1967 (part) from the Palau Is (USNM 11382) on re-examination, are found to be darkly pigmented colonies with a thin layer of pigment and spicules to 0.05mm diameter with conical or blunt-tipped rays, 9–11 in optical section. It appears to be an undescribed species, with some resemblance to *L. cuspidatus*, but with smaller spicules.

Seven species of *Leptoclinides* are recorded exclusively from New Zealand (Millar, 1982). They are not well characterised and are in need of revision. *Leptoclinides sparsus* Michaelsen, 1924 is reported to have spicules to 0.048mm diameter, but the maximum diameter of spicules in the re-examined holotype (ZMC) is 0.035mm. The species is reported to have had black stellate pigment cells in the bladder cell layer. With the exception of *L. volvus* and *L. fungiformis*, Australian species with a preponderance of small (<0.04mm diameter) spicules with regular conical rays (as found in the New Zealand *L. sluiteri* Brewin, 1950b, *L. sparsus* and *L. duminus* Millar, 1982) occur only in the *dubius* group, which is distinguished by its lack of a bladder cell layer and other characters. *Leptoclinides marmoreus* Brewin, 1956, resembles *L. rufus*, but has more coils of the vas deferens and giant spicules have not been recorded. *Leptoclinides auranticus* Brewin, 1956, *L. diemenensis* Michaelsen, 1924 (ZMC holotype re-examined) and *L. novaezelandiae* Brewin, 1958 also resemble *L. rufus*, being distinguished by their smaller spicules and lack of giant ones. They also resemble *L. compactus*, but lack its thick basal test and conical surface protuberances. These characters are used in the key below:

KEY TO NEW ZEALAND SPECIES OF *LEPTOCLINIDES*

1. Spicules to more than 0.035mm diameter 2
   Spicules never more than 0.035mm 5
2. Vas deferens with 9 coils; marbled yellow and grey . . . . *L. marmoreus* Brewin, 1956
   Vas deferens with fewer than 9 coils; not marbled yellow and grey 3
3. Testis 3 or 4 follicles, vas deferens 5 coils; spicules to 0.045mm diameter . . *L. novaezelandiae* Brewin, 1958
   Testis 4 to 6 follicles, vas deferens 6 or 7 coils; spicules to 0.06mm diameter 4
4. Colour orange. . . . . *L. auranticus* Brewin, 1956
   Colour light reddish-grey . . . . *L. diemenensis* Michaelsen, 1924
5. Colony complex with high ridges and protuberances; spicules to 0.035mm diameter . . . . *L. sparsus* Michaelsen, 1924
   Colony not complex with high ridges and protuberances; spicules to 0.025mm diameter. 6
6. Vas deferens 9 coils . . . . . . *L. sluiteri* Brewin, 1950b
   Vas deferens less than 9 coils . . *L. duminus* Millar, 1982

Leptoclinides aciculus sp. nov.
(Figs 11, 159F)

TYPE LOCALITY. Western Australia (24 n miles NNW Port Hedland, 19°57.2'S 118°25.1'E, 20m, coll L. Marsh and M. Bezant on RV Soela 25.9.82, holotype WAM 124.93)

FURTHER RECORDS. Queensland (Whitsundays, off Hook Reef, 31.5m, QM G303827).

COLONY. The surface of the encrusting colony has polygonal elevations, white with spicules, separated from one another by darker depressions (containing some black pigment) over the circular common cloacal canals. The holotype has spicules in small crowded clumps in the raised areas rather than being evenly distributed as they are in the surface test of the Queensland colony. They are in an even layer lining the common cloacal canals, and in a thin and sparse layer on the base of both colonies. The deep circular common cloacal canals around each clump of solid test sometimes occupy the whole depth of the colony but are not posterior abdominal. Zooids are along each side of these canals, their ventral surfaces embedded in the solid test. They are held tightly in these rigid colonies and are impossible to remove

Spicules are stellate to 0.096mm diameter with 9–11 long, conical or chisel-shaped and sometimes, bifid rays in optical transverse section. The ray length/spicule diameter ratio is 0.33.

ZOOIDS. Zooids are relatively small. Branchial lobes were not detected. The atrial aperture is on a short posteriorly directed siphon from the posterior of the thorax. Twelve stigmata are in the anterior row of the branchial sac, 10 in each of the next two rows and 8 in the last row. The distal part of the gut loop is bent ventrally. An ovum and a large testis (consisting of a circle of 5–7 male follicles surrounded by 7 coils of the vas

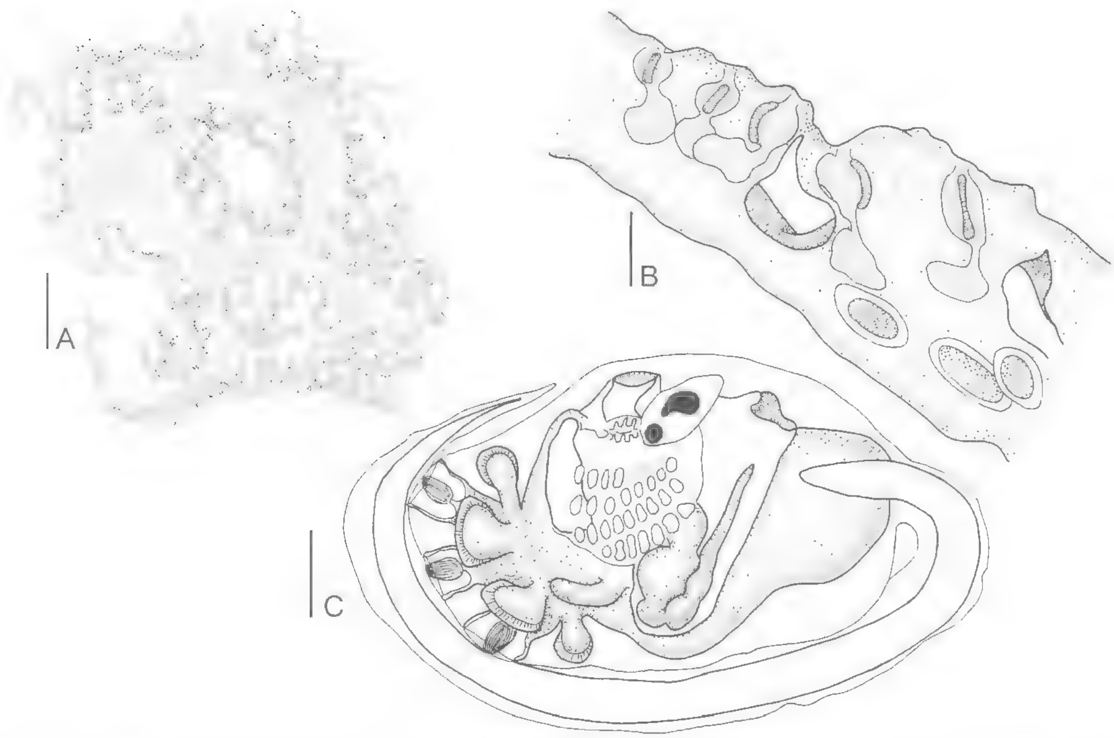


FIG. 11. *Leptoclinides aciculus* sp. nov. (WAM 124.93) – A, surface of colony showing raised areas separated by depressions over primary common cloacal cavities; B, semidiagrammatic section through colony showing deep primary common cloacal canals lined by zooids; C, larva. Scales: A,B, 1mm; C,0.1mm.

deferens) are against the postero-dorsal side of the flexed part of the gut loop.

Embryos and tailed larvae are being incubated in the basal test. The larval trunk is 0.7mm long. Anterior to the oozooid is a spherical reservoir of yolk which decreases in size as the embryo develops. A finger-like external horizontal ampulla projects anteriorly from the vicinity of the larval oesophagus. Six broad, straight-edged epidermal ampullae surround the 3 antero-median adhesive organs. A cap of columnar cells is on the free edge of each ampulla. The usual 4 rows of stigmata are in the branchial sac; and a large ocellus and an otolith are in the cerebral vesicle. The tail is wound three-quarters of the way around the trunk.

REMARKS. Externally the species resembles *L. exiguus* and *L. rigidus* in arrangement of its zooids along each side of primary common cloacal canals which, like the former species, has pigmented test depressed over them. However, the present species has larger spicules than *L. exiguus*. *L. rigidus* has fewer coils of the vas deferens, lacks the bifid spicule rays and has posterior abdominal extensions of its cloacal cavity. *L. maculatus* also has circular primary common cloacal cavities, but these often surround clumps of zooids (rather than zooid-free stands of test with zooids only around the periphery). *L. erinaceus* has larger spicules with more numerous rays. Like *L. seminudus* the present species lacks a posterior-abdominal cloacal cavity, but its larger spicules distinguish it.

Leptoclinides albamaculatus sp. nov.
(Figs 12, 158G;Pl. 1F)

TYPE LOCALITY. Queensland (Heron I., eastern end, low tide, coll. P. Kott 3.9.94, syntypes QM G308274).

FURTHER RECORDS. Queensland (Capricorn Group, QM G301754, G301893, G302974, G308090, G308277, G308291).

COLONY. Colonies are tough, fairly extensive sheets, rather irregular on the surface, with large common cloacal apertures on the highest parts of the colony, i.e. on ridges or other prominences. A surface layer of bladder cells has varying concentrations of black spherical to fusiform pigment cells particularly concentrated around the rims of the common cloacal apertures (which are black owing to the absence of spicules)

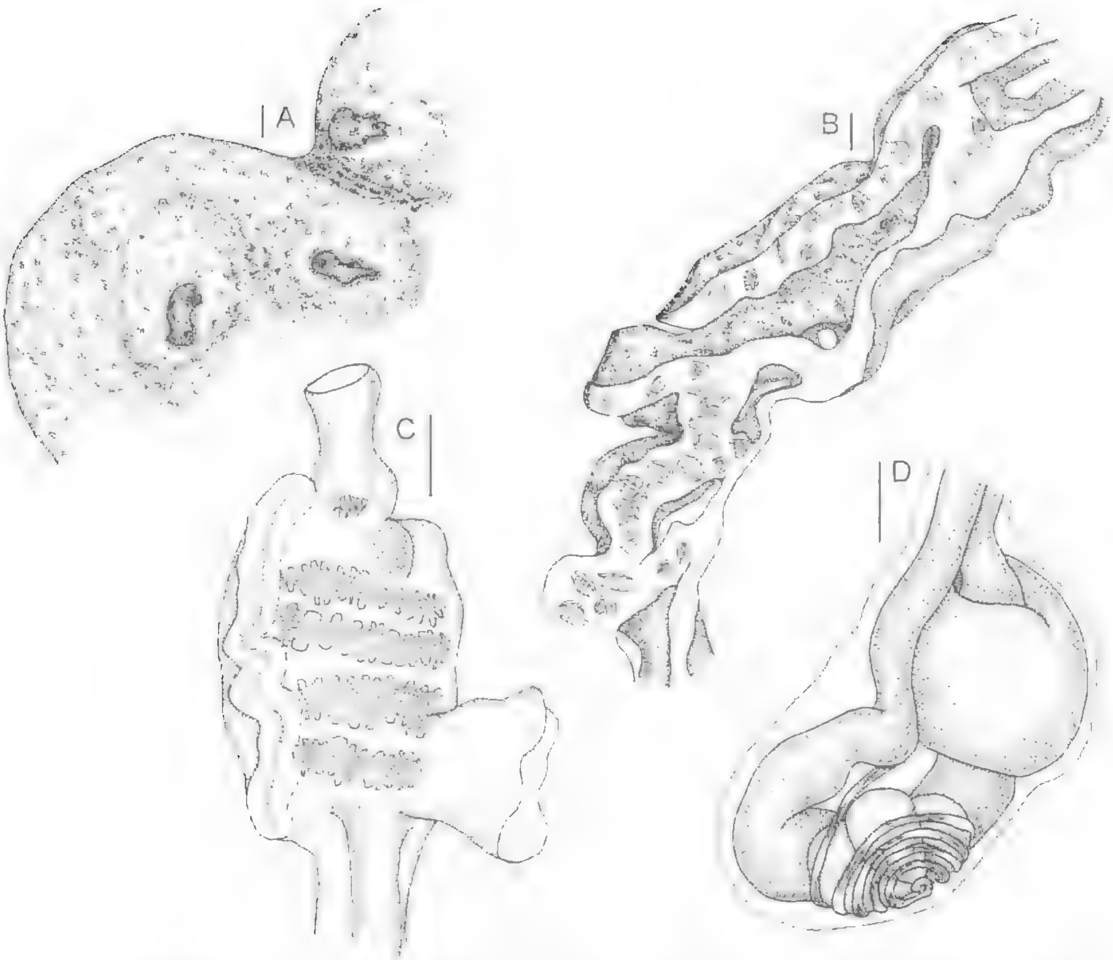


FIG. 12. *Leptoclinides albamaculatus* (A,B, QM G308274; C, QM G308277; D, QM G308291) – A, part of colony from above, showing terminal common cloacal apertures; B, semidiagrammatic section through colony showing zooids embedded in test, and posterior common cloacal cavities (internal and external surfaces shaded); C, thorax; D, gut loop. Scales: A,B, 1.0mm; C,D, 0.1mm.

contrasting with the white lining of the common cloacal cavity that results from the spicules being crowded throughout the remainder of the test. In living colonies, variations in colour from grey to black are associated with differences in this concentration of black pigment in the superficial test. In some parts of the surface the black pigment is interrupted around each branchial siphon and the white spicules are conspicuous, crowded over the anterior surface of the zooids and projecting down into each branchial siphon lining in 3 radial rows. These clumps of white spicules appear as white dots over the surface of the colony.

Spicules, moderately crowded throughout the tough but not brittle test, are up to 0.06mm diameter, with 11–13 moderately long, conical, pointed and sometimes chisel-shaped rays in optical transverse section. Although variable in diameter, spicule shape is particularly uniform. The common cloacal cavity is extensive, and posterior abdominal. Atrial apertures open into the roof of the cloacal cavity, each opening marked by 5 radial rows of spicules. Clumps of zooids, embedded anteriorly in the surface test, are attached to the basal test by single connectives which cross the common cloacal cavity. In life the zooids are white, with some orange-yellow in the abdomen.

ZOOIDS. Zooids are small and very difficult to remove from the test. Four rows of stigmata are in the branchial sac with about 12 in the anterior

row. A large lateral organ is each side of the thorax. Branchial siphons are long, each with a distinct chamber at the base of the siphon causing it to bulge slightly. The rim of the aperture is not lobed. About 4 male follicles have 5 coils of the vas deferens around them. Larvae are not known.

REMARKS. This species looks significantly different from others in the genus owing to its black and white colonies, with conspicuous white dots where the branchial apertures come to the surface. *L. cavernosus* has a similar large cloacal cavity, spicules throughout and 5 radial rows of spicules where the atrial apertures open to the cloacal cavity. However, its zooids are larger than those of the present species, its surface layer of bladder cells is inconspicuous, its spicules are larger with shorter, more numerous and less sharply pointed rays and some yellow and ferruginous pigment is in the surface rather than only the black pigment of the present species.

Leptoclinides carduus lacks a bladder cell layer, has longer and more pointed spicule rays, and orange rather than black pigment is in the surface. *L. rigidus* has similar spicules but they have fewer rays in optical section (7–9) and they are absent from the lower half of the colony. It lacks the black pigment cells in the bladder cell layer, the testis has 8 follicles and the whole colony has a more gelatinous appearance.

Leptoclinides brandi sp. nov.
(Figs 13,159E; Pl. 1G)

Leptoclinides lissus: Brand et al., 1989: 426.

TYPE LOCALITY. Queensland (Heron I., Blue Pools, low tide mark, coll. D. Parry 24.2.82, holotype QM GH918; Heron I., north of island, low tide, under rubble, coll. P. Kott November 1975, paratype QM GH917).

FURTHER RECORDS. Queensland (Capricorn Group, QM GH917-8, GH1831-2, GH4212, G300919-21 G301590, G301891, G302070, G302192, G302957, G302972, G302993, G308104, G308193-6, G308201).

COLONY. Colonies are extensive robust sheets, to 12cm or more. There is no superficial bladder cell layer. The surface of the colony is granular to the touch, owing to the even layer of large spicules crowded in the superficial test. In preserved, possibly slightly contracted specimens, this thin but brittle superficial layer of test, containing the large spicules, looks loose and wrinkled in places. Spicules are present, but sparse, in the remainder of the colony. Often the surface is even, but sometimes it is raised into long anastomosing ridges, with deep depressions between them. Branchial apertures open on both the ridges and in the depressions. In each of the branchial openings are 6 groups or vertical lines of 2–3 crowded spicules, sometimes arranged in a single vertical line. Spicule distribution is continuous from the surface down into the siphon lining and is not interrupted around the aperture. Five radial rows of 2–3 spicules surround each atrial opening into cloacal cavities or canals. Spicules are large (generally about 0.075mm in diameter, and often to 0.1mm), with 9–11 long, tapering, pointed rays in optical transverse section.

Large cloacal cavities open to the surface by randomly distributed apertures. Posterior abdominal canals open into these cavities from the surrounding test. Ridges or other swellings on the surface of the colony are formed where the zooid-bearing layer of test is raised by thickening of the basal test or expansion of the cloacal cavities.

Living specimens are ecru drab[R] with isobella[R] coloured branchial apertures (Ridgeway, 1866), or an off-white colour, sometimes with a greenish tinge conferred by the pale green zooids, and often with patches of brown to green *Prochloron* on the surface. Preserved specimens are white, with translucent test.

ZOOIDS. Zooids have a large (1mm long) thorax. The branchial siphon is short without lobes. The atrial siphon also is relatively short and smooth-rimmed, projecting posteriorly from the postero-dorsal corner of the thorax. A large (to 0.125mm diameter) round lateral organ is each side of the base of the atrial siphon, behind the fourth row of stigmata. There are long pre- and post-stigmatal unperforated areas in the pharynx. Eleven stigmata are in the anterior row. Ventrally, the second and third rows of stigmata are separated from one another by a triangle of unperforated test, the base of the triangle along the endostyle. Stigmata are narrow and fusiform, coming to a sharp point at each end. The gut loop is narrow and relatively straight, and the whole abdomen is bent up ventrally at right angles to the long axis of the zooid. A long duodenum, bulbous distally, opens into a short oval posterior stomach. A mass of gastric tubules are around a constriction about halfway up the rectum. The testis behind the gut loop has a ring of 7 long, almost parallel club-shaped male follicles, their narrow tips converging posteriorly, where they join the vas deferens. The vas deferens makes 5 clockwise coils around the distal half of the follicles. Colonies appear to have either mature testes or ovaries. Colonies collected in November (QM GH917) and July (QM G301891) have

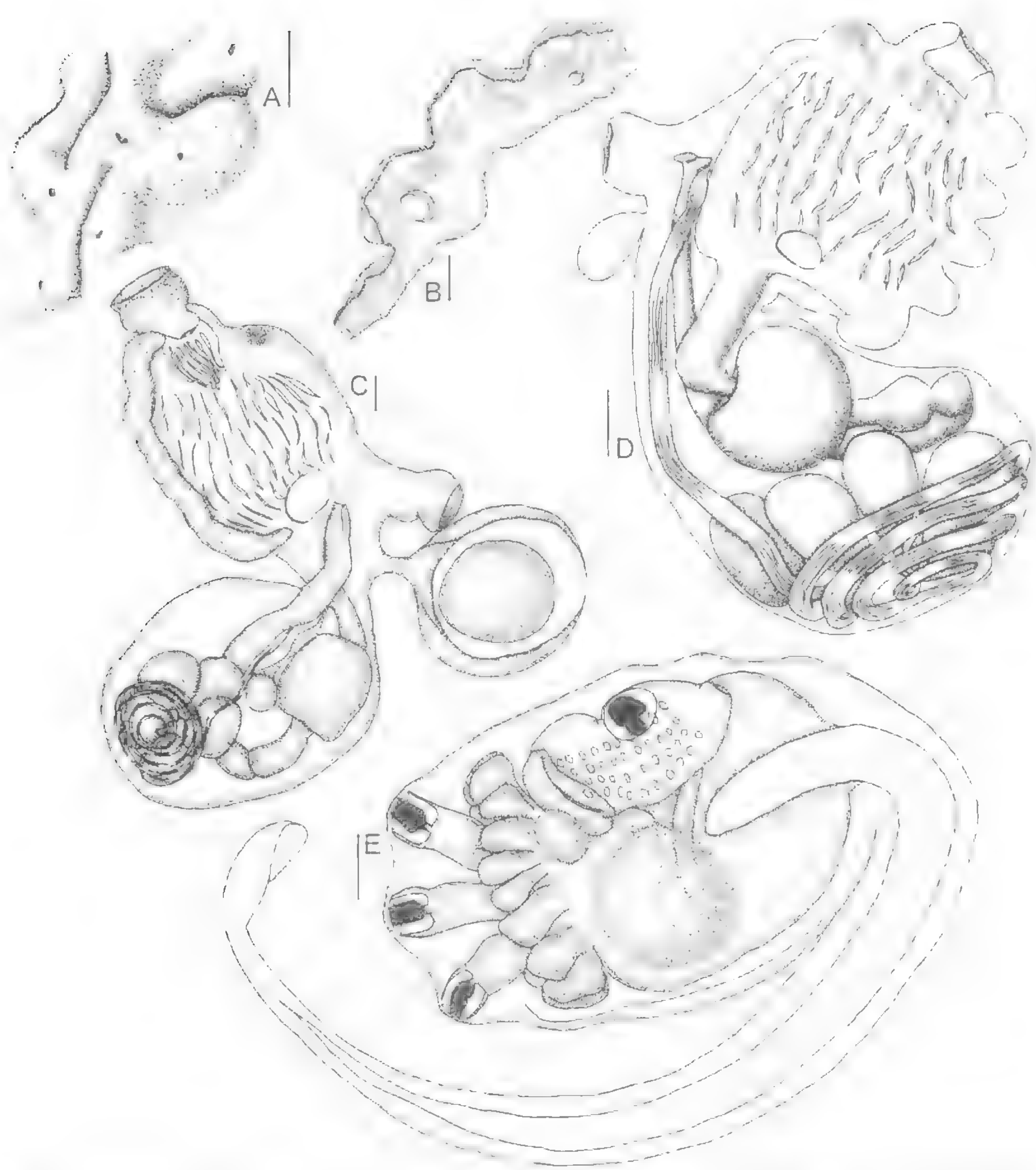


FIG. 13. *Leptoclinides brandi* sp. nov. (A,B, QM GH918; C,E, QM G302993; D, QM GH917) – A, part of surface of a colony; B, semidiagrammatic vertical section through a colony; C,D, zooids; E, larva . Scales: A, 5mm; B, 2.0mm; C–E, 0.1mm.

mature testes, while one taken in February (QM GH918) has an egg at the base of the oviduct just to the left of the testis. A small thoracic brood pouch was present at the base of the atrial siphon in specimens collected in November. Usually one, but sometimes 2 embryos are present in the brood pouches of specimens collected in October (QM G302993). Tailed larvae have a trunk 0.75mm long, with the tail wound about three quarters of the way around it. Eight lateral ampullae are along each side of the antero-median adhesive organs.

Two or three short vascular processes project from the ventral part of the oesophageal neck of the zoid, just anterior to the stomach.

REMARKS. The species is characterised by the absence of a bladder cell layer and pigment cells, and by its large stellate spicules with long, pointed rays forming a brittle layer on the surface of the colony, the 2 or 3 spicules in 3 groups or lines in the branchial siphonal lining, fusiform stigmata, a brood pouch, and the 4 to 7 long vertical male follicles in a single ring.

Leptoclinides marsupialis (Monniot, 1989) from New Caledonia, has similar spicules of the same size, similar fusiform stigmata and a brood pouch, but the colonies are thin, and brittle and appear to have spicules throughout the test. *Leptoclinides apertus* Monniot, 1989 also resembles the present species, differing principally in its lack of a brood pouch, its larger spicules, its yellow-orange to black pigment cells and its 9 coils of the vas deferens. Apparent differences in the atrial siphons of the attenuated zooids of the New Caledonia species are very likely the result of over-narcotisation. *Leptoclinides lissus* also has the abdomen bent up obliquely behind the thorax, similar numbers of testes follicles and vas deferens coils, and stellate spicules crowded at the surface. However, although the spicules are a similar shape to those of the present species they are present throughout the test, are in only 3 (rather than 6) groups of 2 or 3 in the branchial openings, and are only 0.04 to 0.05mm in diameter (less than half the size of spicules in the present species).

Larvae of *Leptoclinides multipapillatus* Monniot, 1989 have even more numerous ampullae than the present species, and their colonies are black in life.

Species of the *dubius* group are readily distinguished from the present species, having testis follicles in a 3-dimensional mass, a range of different types of spicules, and spicules outlining the branchial lobes. With the exception of *Leptoclinides coelenteratus* (which has mostly short-rayed spicules) certain species of the *coelenteratus* group have spicules similar to the present species. However they have a layer of superficial bladder cells which is not present in *L. brandi*.

The vascular processes (stolonic vessels), conspicuous in this species, are also recorded in *L. diemenensis* Michaelsen, 1924 (a species separated from the present one by many characters), and *L. longicollis*. They probably are present in other species in this genus, although generally they are not conspicuous and seldom recorded.

The species is named for Stephen Brand BSc PhD (Qld), whose death in 1992 terminated a promising career in natural products chemistry that had begun with investigations on the inorganic chemistry of this species.

Leptoclinides caelestis sp. nov.
(Figs 14, 160G)

TYPE LOCALITY. Western Australia (Houtman's Abrolhos, Wallabi Group, W. side of Goss Passage, 30-35m, coll. S. Slacksmith and L. Marsh 16.4.78, holotype WAM 794.88).

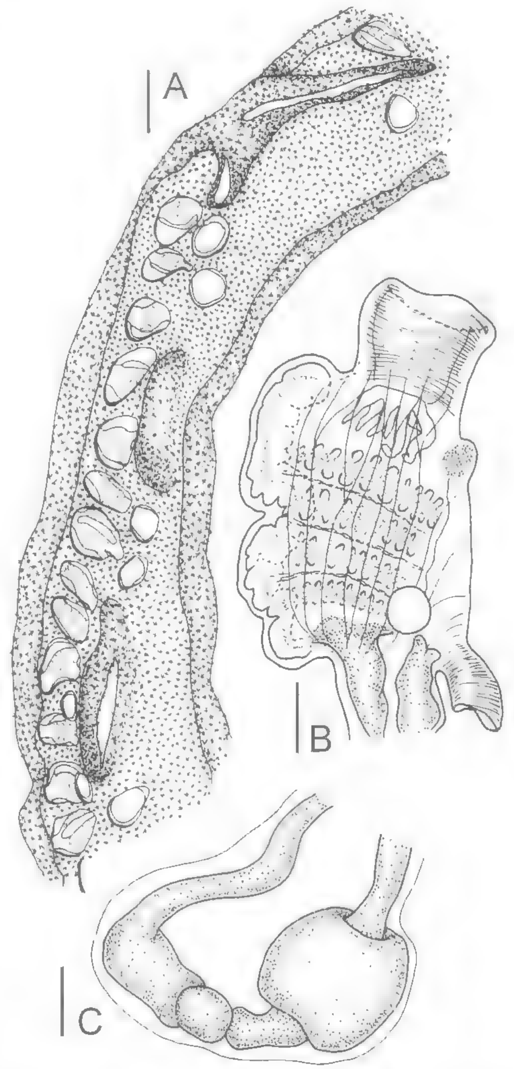


FIG. 14. *Leptoclinides caelestis* sp. nov. (WAM 794.88) – A, semidiagrammatic vertical section through part of colony; B, thorax showing longitudinal muscles; C, gut loop. Scales: A, 1.0mm; B,C, 0.1mm.

COLONY. The colony is a flat sheet with an even surface except here and there where it is raised into shallow domes or protuberances, each with a terminal common cloacal aperture. The test is firm and translucent. Spicules are evenly distributed throughout, and never crowded. Zooids are evenly spaced and visible through the translucent test as dark shadows. Three clumps of spicules form a plug in each branchial siphon. An extensive horizontal common cloacal cavity divides the colony into a zooid-bearing upper layer and a basal layer. The cloacal cavity is interrupted by test connectives between the basal test and the test enclosing groups of zooids at the surface. Atrial apertures open directly into the roof of the common cloacal cavity.

Spicules are large (to 0.15mm diameter) with 7–9 long rays in optical transverse section. A slight variation exists in the length of the rays on one spicule. The ray length/spicule diameter ratio generally is about 0.4, and the form of the spicules is very evident, even at low magnifications.

ZOOIDS. Zooids are relatively small; about 1mm long. The branchial siphon is a wide cylinder, about as long as its diameter. Lobes were not detected around the rim of the aperture. The atrial siphon is short, narrow, and posteriorly directed with 5 minute papillae around its rim. About 10 distinct longitudinal muscles are on each side of the thorax. A small circular lateral organ is on each side of the posterior third of the thorax. The thorax is very contracted in the holotype colony, although in one juvenile thorax it was possible to count 12 oval stigmata in the anterior row. Abdomina appear to be juvenile consisting of a simple, rather open loop, the gut divided into the usual stomach, duodenum, posterior stomach and rectum — the latter constricted about halfway along its length. Gonads are not developed in this colony.

REMARKS. The species is distinguished by its large, spiky spicules, which resemble, but are about five times the diameter of, those of *Leptoclinides echinus* sp. nov. and some of *L. levitatus* sp. nov. However, the present species lacks the other characters of the *dubius* group.

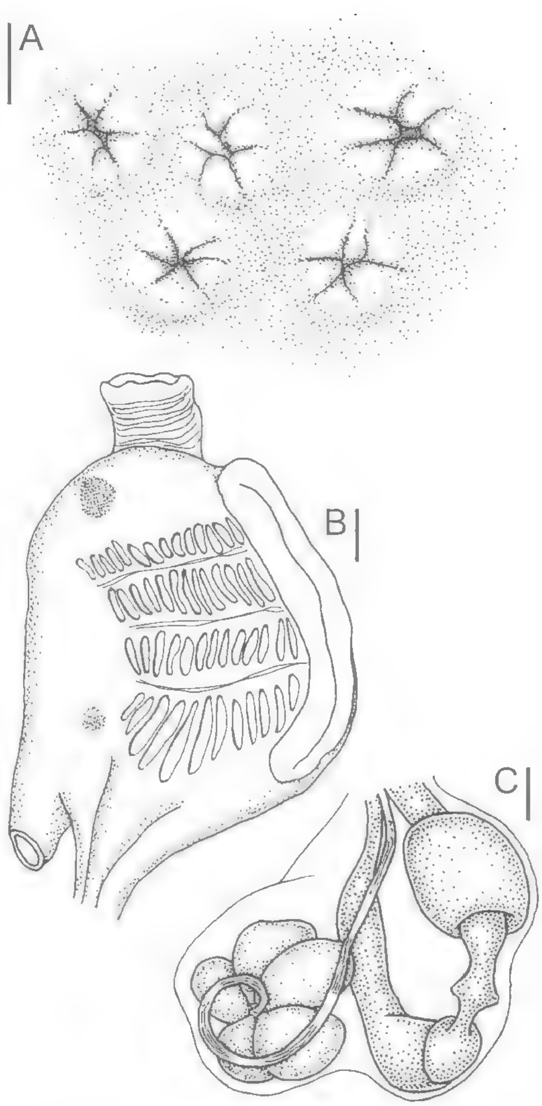


FIG. 15. *Leptoclinides carduus* sp. nov. (QM G308154) – A, surface of part of colony showing branchial apertures; B, thorax; C, abdomen. Scales, A, 0.2mm; B,C, 0.1mm.

Leptoclinides carduus sp. nov.
(Figs 15, 158A)

TYPE LOCALITY. Queensland (Heron I., Coral Gardens, coll. J. Kennedy 8.3.93., low tide, rubble fauna, holotype QM G308154)

COLONY. Colonies are relatively thick (to 5mm) encrusting sheets, with a few common cloacal apertures along the margin of one side. The surface of the holotype is interrupted by evenly spaced, protuberant branchial apertures each with six rows of spicules that appear to be in grooves along the outside of the siphons. In preservative the colony is white, but in life this specimen is orange vermilion[R], the pigment mixed with spicules in the surface. There is no superficial layer of bladder cells.

Large (to 0.075mm diameter) spicules, packed throughout the test, appear almost globular at

lower magnifications but at high magnifications are seen to have about 17–19 rays in optical transverse section. Spicules are of 2 types — the largest are stellate with short conical points, each set in a thicker base, or in the central spherical mass, but the majority are smaller and more burr-like with long fusiform, club-shaped or rod-like rays with pointed, rounded or flattened tips. Common cloacal cavities are extensive and posterior abdominal. Five small groups of spicules are associated with the openings of each atrial aperture in the roof of the common cloacal cavity.

ZOOIDS. Zooids, of moderate size (<2mm overall when relaxed) are difficult to remove from the spicule-hardened test. The rim of the branchial aperture has 6 shallow lobes. A short posteriorly oriented atrial siphon has a small circular lateral organ each side of its base. About 14 round-ended stigmata are in the anterior row in the branchial sac but could not be counted accurately. The gut loop is a relatively straight narrow loop, and the distal part is not flexed ventrally. The gut is divided into stomach, long duodenum, short posterior stomach, and proximal and distal sections of the rectum separated from one another and together forming the ascending limb. The testis, against the dorsal surface of the distal part of the gut loop, is a circle of about 6 oval male follicles. Only a single coil of the vas deferens surrounds it.

REMARKS. The size and form of the zooids and spicules are distinctive. Spicules are relatively large, and their size and form (including the large number of rays in optical section), are unusual in *Leptoclinides*. Hardness of the colonies due to the crowded spicules is also an unusual feature. The spicules with their numerous long, pointed rays, absence of a bladder cell layer superficially, the hard colonies, and the few coils of the vas deferens distinguish the species from *L. cavernosus*, which has a similar cloacal system and spicules throughout. Species in the *dubius* group also have few coils of the vas deferens, however they have a double gut loop, a false siphon at the base of the branchial siphon, and smaller spicules absent from much of the colony — characters that distinguish them from the present species.

Leptoclinides cavernosus sp. nov.
(Figs 16, 158-I; Pl. 1H)

Askonides imperfectus Kott, 1962: 294 (part, specimen from Switzer Reef).

TYPE LOCALITY. Queensland (Heron I., N of meteorological tower, rubble zone, coll. P. Kott, March 1975, holotype QM G300896; Heron I, Blue Pools, coll. P. Kott 9.11.85, paratype QM G302102).

FURTHER RECORDS. Western Australia (Exmouth Gulf, QM G302942). Queensland (Heron I., QM G301570, G301579, G301582, G301920, G301940, G302021, G302130, G302532, G302541, G302961, G302969, G302978, G302985, G308059-62, G308066, G308098, G308237, G308247, G308282, G308284, G308292, G308307). Coral Sea (Marion Reef, QM GH305; Switzer Reef – AM Y1349 Kott, 1962).

COLONY. Colonies invest hard substrates. The surface sometimes is raised into regularly spaced, rounded domes about 4–5mm in diameter, with terminal common cloacal apertures (QM G300896, G301940) or lobes with terminal apertures (QM G308247). Often surface swellings are less regular. A large colony (QM G302985) is about 20cm in maximum extent. Some small colonies, each consisting of a single system with a central cloacal system, were taken on *Halimeda* (QM G308292). Some colonies (QM G301579) have part of the upper surface flat and even, with sessile cloacal apertures randomly placed, or they have long or irregular and convoluted surface swellings with one or more large, open, white-rimmed cloacal apertures on them. Cloacal apertures are not in the depressions between the surface swellings. The cloacal apertures are often very large, wide openings, although in preserved specimens these may be partly closed with a frilled rim in which some black pigment persists.

A thin superficial layer of bladder cells has spicules and pigment cells embedded in it. A layer of crowded spicules is beneath the bladder cell layer and spicules are present throughout the remainder of the test in moderate concentrations. Open common cloacal cavities are beneath the apertures and around these cavities, especially around the margins of the colony, the test is penetrated by narrow canals at abdominal level that surround clumps of zooids. A circular spicule-free area surrounds each branchial aperture. Two or three spicules are crowded into 3 –6 groups or 3 radial lines in the lining of each branchial siphon, often forming a plug in the aperture. Five lines of spicules extend into the atrial siphons marking their openings into the cloacal cavities. Spicules are large, stellate, to 0.13mm diameter. They have 13–15 sharply pointed to chisel-shaped conical rays in optical section, although some spicules have blunt, round-tipped rays.

Living colonies are said to have had brown, black and yellow pigment cells in the surface

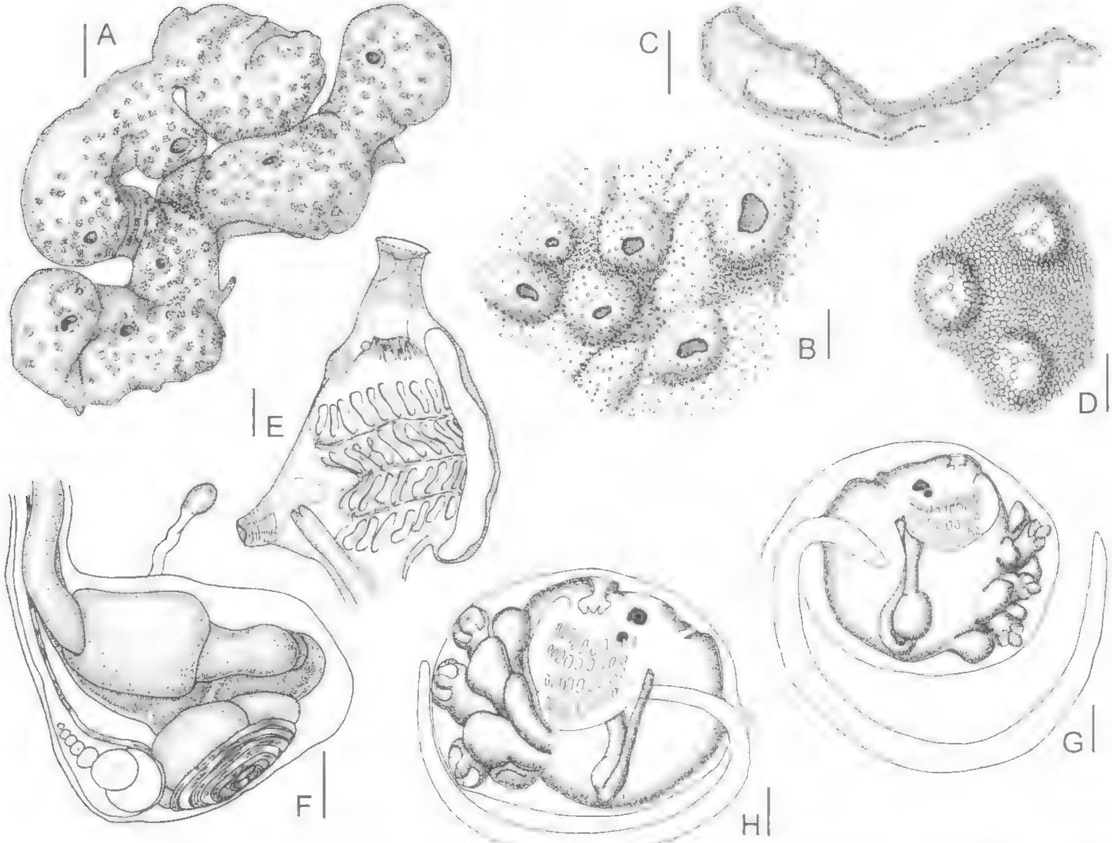


FIG. 16. *Leptoclinides cavernosus* sp. nov. (A,E, QM G301940; B–D, QM G300896; F, QM G302942; G, QM G302532; H, QM G301579) – A,B, portions of colonies, from upper surface showing terminal common cloacal apertures on surface elevations; C, semidiagrammatic vertical section through part of colony showing large posterior abdominal cloacal cavity beneath terminal aperture; D, semidiagrammatic view of branchial apertures from surface showing 3 radial rows of spicules in each siphon lining; E, thorax; F, abdomen; G,H, larvae. Scales: A–C, 2.0mm; D, 0.2mm; E–H, 0.1mm.

mixed with spicules and to have been ferruginous[R], mummy-brown[R], drab[R], drab[R] with sage green[R], green and white, dark brown, burnt amber[R] with fawn, and mottled purple and white with straw yellow[R] around the edges of the colony and on the cloacal apertures. Several colonies had black pigment in the surface test, and yellowish zooids, one colony was very white around the apertures with dark brown pigment mixed with spicules in the remainder of the surface test, and several colonies (QM G300896, G308247) are said to have been orange with more intense colour around the terminal common cloacal apertures. In one living colony (QM G308307) crimson[R] pigment cells with some splashes of yellow were noted. In preservative colonies are pale tan to beige in the surface, with flecks of orange pigment in the surface bladder cell layer, mixed with some spicules, or they are white with some irregular black pigment in the bladder cell layer, or slightly translucent and pinkish-white.

ZOOIDS. Zooids, relatively small with narrow thoraces up to 1mm long when not contracted, are removed from the test only with the greatest difficulty. The atrial siphon, directed posteriorly from the postero-dorsal corner of the thorax, is relatively short. The branchial siphon often is funnel-shaped, contracted around the base and with branchial tentacles sometimes projecting forwards in a chamber in the lower half of the siphon. Branchial lobes are shallow, and atrial lobes were not detected. A large, shallow, plate-like lateral organ is each side of the base of the atrial siphon. A simple duct from the neural gland opens into the dorsal mid-line of the

pharynx behind the branchial tentacles. Three large dorsal languets are to the left of the dorsal mid-line. The branchial sac has 10 stigmata in the first row. A simple gut loop has the usual smooth spherical stomach, long duodenum, oval posterior stomach in the pole of the loop. The ascending rectum is wide at its proximal end and, about halfway up where its diameter decreases, tubules of the gastro-intestinal gland surround it. Four to 6 club-shaped testis follicles are in a ring, their narrow ends converging to the vas deferens which coils 6 times around the outside of the testis. Abdomina are bent up to the left of the thorax in the upper half of the colony.

Embryos are in the basal layer of test, beneath the cloacal cavities, in a colony (QM G301579) collected at Heron I. in August. Larvae have a trunk about 0.7mm long, with 2 lateral ampullae on each side, and a median-dorsal and a median-ventral ampulla. A short anteriorly directed horizontal digitiform lobe projects from the left side of the larval trunk near the base of the lateral ampullae.

REMARKS. The species resembles *L. coelenteratus* from Western Australia, differing in its less developed cloacal cavities, smaller zooids, and a larval trunk about half the length of *L. coelenteratus*. The spicules are similar with the same size range and even distribution through the test, although *L. coelenteratus* has spicules with slightly fewer rays than the present species.

Protuberant cloacal apertures are similar to some in the *dubius* group, although the characters of the *dubius* group are not present in *L. cavernosus*.

L. cavernosus is distinguished from *L. rufus* by its very much less conspicuous surface layer of bladder cells, spicules throughout the colony (rather than being confined to a layer beneath the bladder cells), and its very large, oval, lateral organ. The spicules have fewer rays than in *L. rufus* (which also has occasional giant spicules). *L. imperfectus* has similar cloacal systems, relatively small zooids and occasionally has large spicules (to 0.1mm) as in the present species. However, it has even smaller, distinctively shaped zooids with a long oesophagus, it lacks a bladder cell layer and generally has fewer spicule rays in optical transverse section (about 9).

Leptoclinides coelenteratus (Kott, 1962)
(Figs 17, 159C; Pl. 2A)

Askonides coelenteratus Kott, 1962: 292 (part, not specimen from Green Pools); 1998: 86.

PREVIOUSLY RECORDED. Western Australia (Rottnest I. – AM Y1344, Y1345, Y1347 Kott, 1962; Point Peron – holotype AM Y1343 Kott, 1962..

DESCRIPTION. COLONY. Colonies are robust, the upper surface raised into hemispherical domes about 4mm in diameter with central common cloacal apertures which often are raised on funnels or chimneys. The base of the colony is flat although prop-like roots sometimes extend from it. Spicules are moderately crowded throughout, being present in the superficial layer amongst the bladder cells, as well as around the zooids and in the base of the colony. Branchial apertures are conspicuous on the surface, with each of the 6 lobes associated with a patch of spicules. Colonies are white in preservative. Cloacal cavities are large occupying the centre of each surface dome. Atrial apertures, opening directly into the ceilings of these cavities, are made conspicuous by the 5 double rows of spicules in the test lining each aperture. Spicules are to 0.06mm, rarely to 0.08mm, in diameter. Most have 11–13 relatively short pointed conical rays in optical transverse section but some have fewer. Some of the smaller spicules have blunt rays, and some are almost globular.

Zooids around the margins of the cloacal cavities are stretched out, with abdomina in the basal test. The other zooids in the test over the cloacal cavities have abdomina bent up alongside the thoraces.

ZOOIDS. Zooids are about 2.5mm long with an atrial siphon about 1mm long extending from the postero-dorsal corner of the thorax. The rim of the branchial aperture has 6 short points and that of the atrial aperture has 5 small, narrow ones. A narrow sphincter muscle is around the atrial aperture and the test of the siphon has only delicate and sparse circular muscles. About 12 fine longitudinal muscle bands are in the parietal body wall. A large, plate-like lateral organ (to 0.1mm in diameter) is invaginated into the body wall on each side of the base of the atrial siphon opposite the fourth row of stigmata. The branchial siphon is relatively long and in some specimens the anterior part of the body is produced forwards so that the branchial tentacles appear to be in an expanded chamber near the base of the siphon. An extensive pre-branchial area is anterior to the particularly long and narrow stigmata, pointed at each end, in 4 rows of up to 15. The gut loop is narrow and more or less straight and vertical. The stomach is large and smooth, the duodenum wide, and a small oval posterior stomach is in the pole of the gut loop.

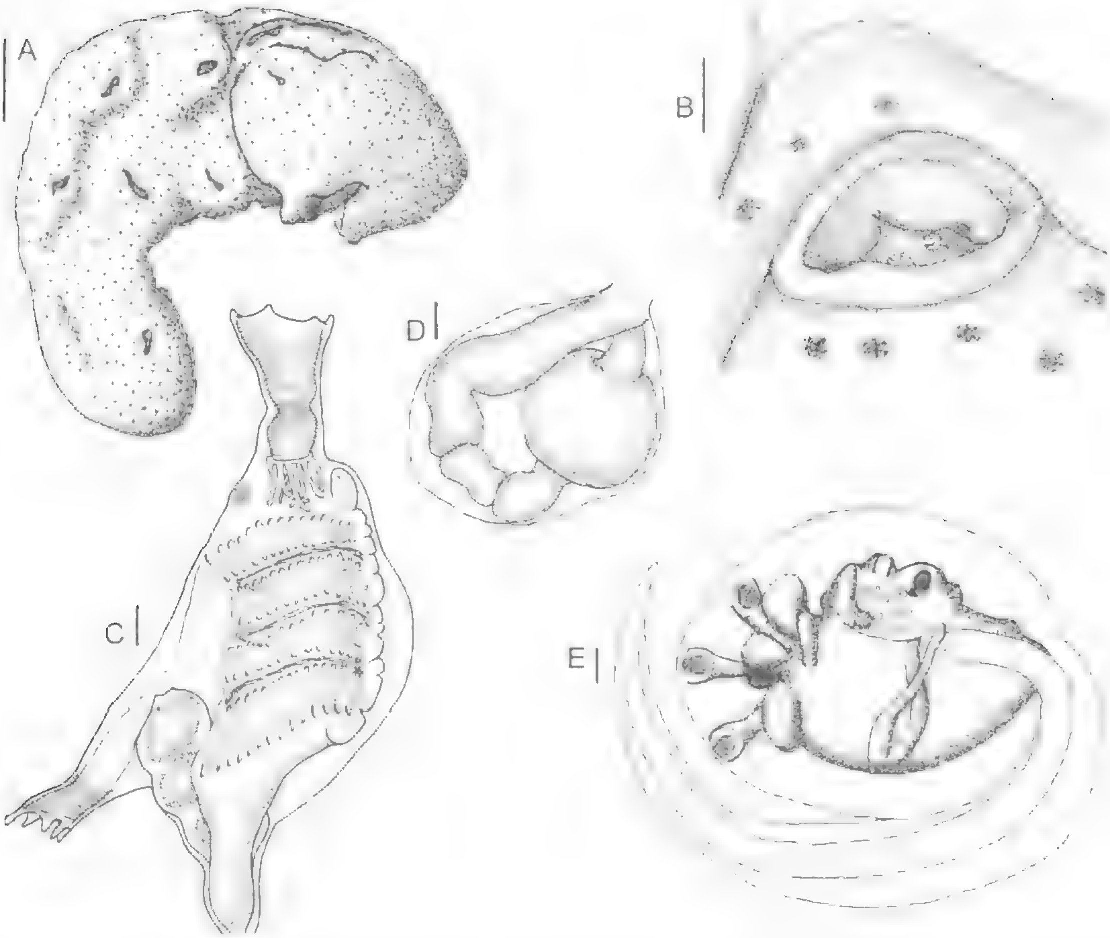


FIG. 17. *Leptoclinides coelenteratus* (AM Y1345) – A, colony; B, common cloacal aperture showing a few of the 5 lobed atrial apertures opening into the cavity; C, thorax; D, gut loop; E, larva. Scales: A, 0.5mm; B, 1.0mm; C–E, 0.1mm.

The wide rectum curves into the base of the atrial siphon. Kott (1962) describes the testis as a ring of about 6 follicles, with 4½ coils of the vas deferens around its outer surface. Gonads are not present in the re-examined material.

Larvae, in the basal test of a specimen (AM Y1345) collected in November, are large, the trunk being 1.1mm long. They have one lateral ampulla on the left, 2 on the right and a median dorsal and a median ventral ampulla. A forward-pointing accessory ampulla extends from the left side of the waist of the larval trunk.

REMARKS. The principal characteristic of this species is its large, open cloacal cavities into which the 5-lobed atrial siphons open directly. Its spicules, evenly distributed throughout (including the superficial layer of test where they are mixed with bladder cells) and large larvae are also distinctive. Kott (1962) referred to spicules up to 0.08mm in diameter. Spicules of maximum size are rare in the re-examined material. *L. rufus* has some large cloacal cavities with zooids opening directly into them. However, its larvae are smaller, atrial apertures lack the 5 lobes and, although a similar shape, generally the spicules are smaller (to 0.05mm) and present in a single layer beneath a conspicuous superficial bladder cell layer. Giant spicules sparsely but evenly distributed in *L. rufus*, do not occur in *L. coelenteratus*.

L. cavernosus resembles the present one most closely. Its spicules are the same size although the conical rays tend to be longer than those in the present species, it has similar numbers of testis

follicles and vas deferens coils, and it sometimes has 5 minute atrial lobes. However, it has smaller zooids, only 3 clumps of spicules in each branchial aperture, shorter atrial siphons, less crowded spicules, smaller larvae and its surface is not raised into such high domes as in the present species. *L. cavernosus* is recorded from NE Australia while records of the present species are from Point Peron-Rottnest I., Western Australia.

The present species has some resemblance to *A. tubiporum*. However, even in the absence of gonads to support the generic difference, *L. coelenteratus* colonies are not produced into such markedly cylindrical lobes, its spicules are generally smaller and its atrial siphons shorter.

Leptoclinides comitus sp. nov.
(Figs 18, 157H)

TYPE LOCALITY. Tasmania (Port Davey, Bathurst Channel, off Eve Point, rock slope with *Hormosira*, 1-10m, WEB statn 6, coll. W. Zeidler, K.L. Gowlett Holmes, F.A. Bavendan 7.4.93., holotype SAM E2614; paratype SAM E2615).

COLONY. Colonies are fleshy investing sheets with a single superficial layer of moderately crowded spicules at the surface of the colony and few elsewhere. The test is soft and translucent. Colony SAM E2615 is particularly irregular, investing rubble, and the spicules are less crowded than in the holotype. Branchial siphons protrude slightly from the surface like small warts. Spicules are most crowded where the surface layer of test with its contained spicules curves in to line each branchial siphon, creating white dots where the zooids open to the surface. Spicules are mostly globular with crowded flat- or round-tipped rays, but some are stellate. They are very variable in size, up to 0.07mm in diameter, but most are smaller.

Common cloacal cavities are deep around each group of zooids but do not extend into posterior abdominal cavities except in the vicinity of common cloacal apertures, where the size of the cavity increases. Abdomina are embedded in the basal test but the basal test beneath the deep cloacal cavities around each group of zooids is particularly thin and clumps of abdomina protrude into the cloacal cavity.

ZOOIDS. Zooids are small, with a small thorax and a wide rather trumpet-shaped, flaring atrial siphon. A copepod (with nauplius larvae) is in the gut loop of all examined zooids in the holotype and in many zooids of the paratype. A small circular lateral organ is on each side of the mid-thorax. Small, narrow columnar epithelial cells project from the body wall, especially the anterior thoracic wall and the outside of the branchial siphon. The branchial aperture has 6 short points around its rim. The oesophageal neck is long and the gut forms a simple vertical loop. The usual duodenum is behind the stomach, opening into the wide posterior stomach that increases its diameter to the large proximal part of the rectum in the pole of the gut loop. The distal part of the rectum is not appreciably narrow in these zooids owing to the copepods in the gut. The testis, well developed in zooids of the paratype, consists of up to 8 follicles surrounded by 2 coils of the vas deferens. Larvae are not known for this species.

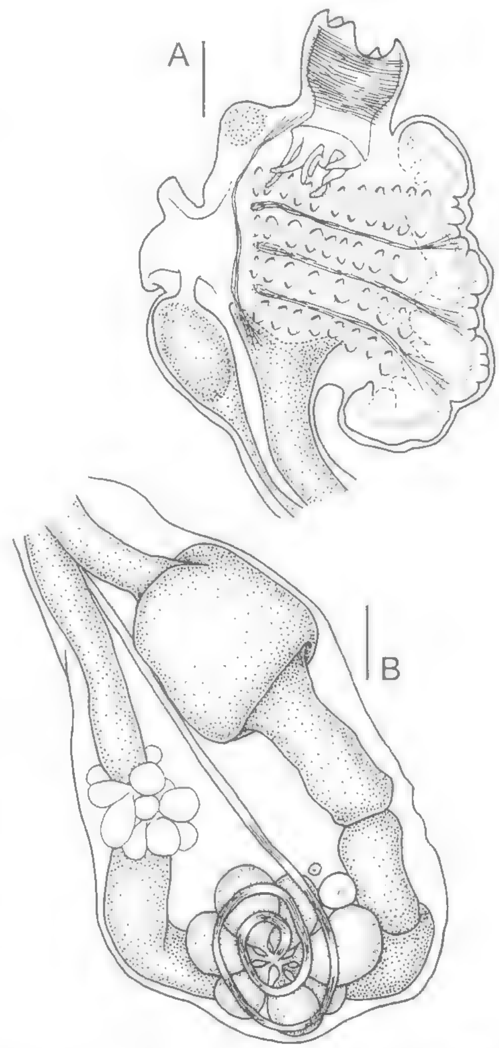


FIG. 18. *Leptoclinides comitus* sp. nov. (SAM E2615) – A, thorax; B, abdomen. Scales: 0.1mm.

REMARKS. Although both species have similar translucent colonies with the spicules confined to a layer in the surface the present species is distinguished from *Didemnum pellucidum* by its generic characters as well as its variable sized, often globular, spicules.

The species resembles *Polysyncraton circulum* in the distribution of its spicules and in the form of the cloacal systems but the large muscular atrial siphon of *Leptoclinides* readily distinguishes it. The species is unusual in its globular spicules as most species of this genus, except the tropical *L. carduus*, have large stellate ones. *L. carduus* also has a similar testis but with only one coil of the vas deferens and its spicules are crowded throughout, unlike those of the present species.

Leptoclinides compactus sp. nov.
(Figs 19A, 160D; Pl. 2B)

Leptoclinides rufus: Kott, 1975: 8 (part, specimens from outside bar).

Polysyncraton paradoxum: Kott, 1972b: 178.

TYPE LOCALITY. South Australia (Price I. Avoid Bay, Great Australian Bight, coll. S.A. Shepherd et al., 9.4.87, holotype QM G302052; Perforated I., coll. S.A. Shepherd et al., 8.4.87, paratype QM G301589).

FURTHER RECORDS. South Australia (Elliston Bay – SAM E2626, QM G8580 Kott, 1972b; SAM E2635-6, Kott, 1975).

COLONY. Colonies form extensive, tough, but not brittle, sheets (from about 5mm thick) with irregular conical prominences (to 1cm high) each with a terminal cloacal aperture. A relatively thick superficial layer of bladder cells only occasionally contains some spicules. Deep, vertical cloacal cavities surround clumps of about 15 zooids, and penetrate amongst them at oesophageal level. Sometimes the deep primary cavities extend into posterior abdominal spaces, especially beneath the cloacal apertures which are raised above the surface of the colony. Sometimes these surface prominences are created by thickening of the basal test, but others are the result of an increase in the size of cloacal cavities. Spicules are crowded beneath the superficial bladder cell layer and extend into it around each branchial siphon. They become less crowded beneath the common cloacal cavities and with the exception of the base of the colony (where sometimes there is a single layer), spicules are generally absent from the lower half of the colony. This spicule-free lower part is of variable thickness — from half to more of the thickness of the colony. Spicules are of moderate size (occasionally to 0.06mm diameter) with conical pointed rays, sometimes truncated and sometimes with chisel-shaped tips, about 9–11 in optical transverse section. Small groups of 2 or 3 spicules are in 3 clumps or lines in the lining of each branchial siphon. A clear spicule-free area over the anterior end of each zooid separates these groups of spicules from those in the rest of the surface.

Colonies from Elliston Bay are said to have been orange in life.

ZOOIDS. Zooids are small,. less than 1.5mm long, with the thorax only about two-thirds of the length of the abdomen. They are not readily removed from the tough test. A large, flat circular lateral organ is in the centre of each side of the thorax opposite the last row of stigmata. Only about 8 stigmata are in each of 4 rows in the branchial sac. The atrial aperture is on a short posteriorly directed siphon from the postero-dorsal corner of the thorax. The gut forms a relatively narrow vertical loop. The stomach is long and narrow, the duodenum is relatively short and a small oval posterior stomach is in the pole of the gut loop. The testis consists of up to 7 pear-shaped follicles in a ring, with 6 coils of the vas deferens around its outer half. Larvae are not known.

REMARKS. Characteristics of the species are its thick layer of bladder cells on the upper surface and the relatively few stigmata in each row in the branchial sac. Of the species with spicule-free superficial layers of bladder cells like the present one, *L. exiguus* has more restricted cloacal systems and larger spicules, and *L. rufus* has a distinctive colour pattern and giant spicules regularly scattered amongst the others. *L. maculatus* has similar spicules with a similar distribution to those of the present species. These species are distinguished from the present one by their colour patterns and relatively even upper surfaces without protuberances. Another South Australian species, viz. *L. imperfectus*, has spicules in the superficial layer of test, more numerous testis follicles and vas deferens coils, and does not appear to be the orange colour of the present species. Also it has surface prominences with terminal cloacal apertures in the centre of enlarged cloacal cavities rather than having prominences supported by a solid core of basal test. *L. longicollis* from Moreton Bay has a similar colony and spicule form and distribution, but it has larger zooids and it lacks chisel-shaped spicule rays. The tropical *L. sulawesii* has surface

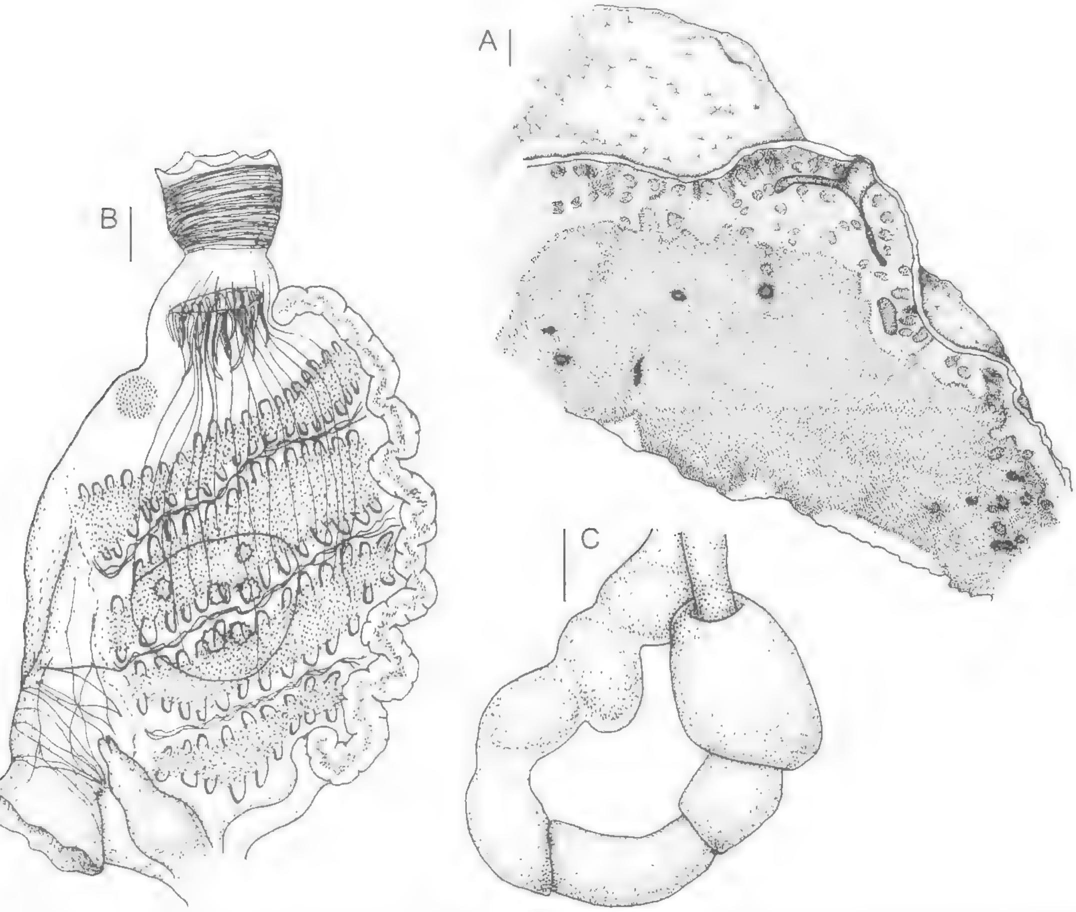


FIG. 19. A, *Leptoclinides compactus* sp. nov. (QM G302052) – A, semidiagrammatic vertical section through a common cloacal canal showing superficial bladder cell layer, zooid layer and thick basal layer of test. B,C, *Leptoclinides confirmatus* sp. nov. (SAM E2619) – B, thorax showing parietal longitudinal muscles; C, abdomen. Scales. A, 1.0mm; B,C, 0.1mm.

elevations with terminal common cloacal apertures, although these may be lower than those of the present species and it has spicules with fewer rays.

In the 2 extensive colonies assigned to the New Zealand species, *Polysyncraton paradoxum* by Kott (1972b) the thoraces are mostly in regressed condition, the atrial siphon of *Leptoclinides* was not observed, and common cloacal cavities are not present in either of the colonies. However one juvenile thorax with the relatively few stigmata (8) in each row was found, and they have characteristic spicules with chisel-shaped rays, spicule-free layers in the colonies, male gonads with 6 coils of the vas deferens, and a simple vertical gut loop. These colonies are now assigned to the present species.

Leptoclinides confirmatus sp. nov.
(Figs 19B,C, 158C)

TYPE LOCALITY. Tasmania (Port Davey, Bathurst Channel off Jean Point, steep rock slope 21m, WEB statn 5, Coll. W. Zeidler, K.L. Gowlett Holmes, F.A. Bavenden 5.4.93, holotype SAM E2619.)

COLONY. The colony is tough and encrusting with some ridges and furrows and irregularly distributed low elevations on the upper surface, each with a permanently open cloacal aperture. Spicules are crowded in the superficial layer of test, and there is no layer of bladder cells. Branchial apertures are obscured by the spicules crowded in the test which is slightly elevated over each aperture. Large spicules to 0.14mm in diameter, with 13-15 relatively short conical rays in optical section are present throughout the test, although never as crowded as in the superficial

layer. The ray length/spicule diameter ratio is not more than 0.27. Common cloacal cavities are generally posterior abdominal expanding beneath the apertures, to cause surface elevations.

ZOOIDS. Zooids are large (to 3mm long) with about 20 stigmata per row in the large thorax. Branchial apertures are on a long, muscular siphons, each with 6 small pointed lobes on the rim of the opening. A large plate-like lateral organ to 0.25mm diameter is on each side of the posterior end of the thorax. The atrial siphon is posteriorly directed, but relatively short. Papillae were not detected on its rim, but zooids were difficult to remove from the colony and they may have been torn off. Twenty long, narrow stigmata are in the anterior row. The abdomen is about the same length as the thorax, the oesophageal neck being quite long. The distal part of the gut loop is slightly flexed. Gonads were not detected in the holotype.

REMARKS. Although gonads have not been detected in the holotype, the large zooids with their posteriorly oriented atrial siphon, and robust colonies with terminal common cloacal apertures on elevated parts of the surface over large cloacal chambers are characteristic of *Leptoclinides*.

Large, stellate spicules in the superficial layer of test, making it hard and raspy, distinguish this from other temperate species. Similar but not such large spicules are in tropical *L. cuspidatus* and *L. apertus*, although their spicule rays are longer, more pointed and fewer, and fewer stigmata are in the branchial sac.

The colony from Oyster Bay Tasmania (AM Y1481) assigned to *Polysyncraton mortenseni* by Kott (1962) is robust, growing over a bryozoan colony. Unfortunately the zooids have disintegrated in this colony. It has an extensive posterior abdominal cloacal cavity, and probably posteriorly oriented atrial apertures opened into it. The posterior abdominal space has various strands of spicule-filled test, joining the surface layer of test to the thin layer of basal test which adheres to bryozoans and weed stalks. Kott was wrong in her suggestion that the posterior abdominal spaces are not part of the cloacal system, as interruptions in the test where atrial apertures were located can be detected. Although its stellate spicules reach more than 0.1mm in diameter, as in the present species, they have fewer rays. The specimen appears to be a distinct, apparently previously undescribed, species of *Leptoclinides* with 5 or 6 testis follicles surrounded by 3 or 4 coils of the vas deferens (Kott, 1962), viz. *L. magnistellus*.

Leptoclinides constellatus sp. nov.
(Figs 20, 160A; Pl. 2C)

TYPE LOCALITY. Queensland (Whitsunday Group, Haselwood I., bay NNE of small island in Solway Pass 15m, coll. AIMS Bioactivity Group 18.11.88, holotype QM G302924; Keswick I., side of channel between Keswick I and St Bees 0m, coll. AIMS Bioactivity Group 14.11.88, paratype QM GH5420).

COLONY. In preservative, colonies are extensive fleshy sheets to 5mm thick with slightly elevated opaque oval areas, sometimes zooid-free but some with clumps of zooids, surrounded by depressions over primary common cloacal canals that are lined on each side by zooid openings. Sometimes posterior abdominal cavities continuous with the primary cavities extend beneath clumps of zooids and their posteriorly oriented atrial siphons often open directly into these cavities. Spicules are present beneath a relatively conspicuous superficial layer of bladder cells. They become less crowded around the zooids, and except for single layers lining the common cloacal canals and on the base of the colony, spicules are absent from the lower half of the colony. Crowded bladder cells are in the central test. Spicules are stellate, to 0.07mm diameter with 9–11 conical rays in optical transverse section. The rays have sharply pointed or chisel-shaped tips and some are shorter and truncated. The living colonies are said to have been beige/tan, with a shiny smooth surface. In preservative they are a dirty beige colour.

ZOOIDS. Zooids are large, the thorax, being to 1mm long. The abdomen (including the oesophageal neck) is about the same length and is bent at right angles to the longitudinal axis of the thorax. Neither branchial nor atrial siphons have lobes on the rims of the apertures, and both are relatively long. The branchial sac has 12,10, 9 and 8 stigmata respectively in the first to last rows. The oesophageal neck is relatively short, being less than half the total length of the abdomen. The testis has 5 or 7 follicles arranged in a circle, and the vas deferens coiled 6 times around their upper surface. Larvae are not known for this species.

REMARKS. The species resembles the sympatric *L. rigidus* in both its spicules and their distribution and in the form of the colony and its cloacal systems, the latter having simple, deep primary canals with zooids lining them and large

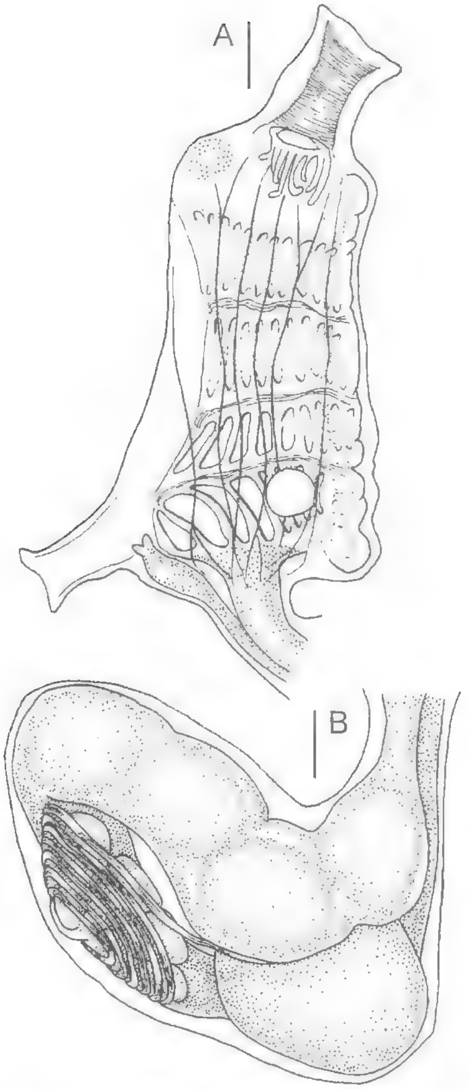


FIG. 20. *Leptoclinides constellatus* sp. nov. (QM G302924) – A, thorax showing parietal longitudinal muscles; B, abdomen. Scales: 0.1mm.

horizontal posterior abdominal cloacal spaces behind clumps of zooids. The most significant and consistent differences from *L. rigidus* are 6 vas deferens coils (rather than 5), fewer stigmata (the maximum number per row being 12 rather than 15), shorter oesophageal neck and smaller spicules with fewer rays. *L. maculatus* is distinguished by its more numerous spicule rays. *L. seminudus* and *L. sulawesii* have similar spicules, but the former has 8 coils of the vas deferens and the latter has different cloacal systems and different colonies with rounded elevations on the surface.

Leptoclinides cuspidatus (Sluiter, 1909)
(Figs 21, 158H; Pl. 2D)

Didemnum cuspidatum Sluiter, 1909: 57.
Didemnum reticulatum Sluiter, 1909: 60 (part, 1 of 2 specimens from Siboga statn 322).
Leptoclinides oscitans Monniot & Monniot, 1996: 177.

NEW RECORDS. Western Australia (north of Barrow Is, QM G300956). Queensland (Little Broadhurst Reef, QM GH5348; Murray I., QM GH383). Philippines (off Dumaguete Airport runway, QM G302893, G300939).

PREVIOUSLY RECORDED. Indonesia (part *Didemnum reticulatum* Sluiter, 1909 ZMA TU475.9; syntypes *Didemnum cuspidatum* Sluiter, 1909, ZMA TU440.1, TU440.2; Monniot & Monniot, 1996). Palau Is (Monniot, & Monniot, 1996).

COLONY. Specimens are solid cushions to 2cm in maximum dimension or more extensive relatively thin sheets with rounded margins. The specimen from Murray I. is a small upright lobe, about 5mm in diameter, with a terminal aperture and a central common cloaca, fixed by its posterior end and part of one side. In the larger sheets, numerous protuberant common cloacal apertures are evenly spaced over the surface with black pigment showing through the cloacal aperture and with a relatively shallow posterior abdominal common cloacal cavity. The black pigment is in long, or branching bodies or sometimes spherical cells. Sometimes it is mixed with spicules in parts or the whole of the superficial test resulting in black and white marbled or entirely grey to black colonies respectively. In the white patches the pigment does not occur in the superficial test at all. Pigment is always present beneath the sometimes crowded surface layer of spicules, around the zooids and in the roof of the cloacal spaces. Toward the base of the colony the pigment is more sparse and is in fusiform cells.

Large (to 0.125mm diameter) stellate spicules are present in the surface layer of test. Also, a single layer of moderately crowded spicules is on the base of the colony. In the larger colonies only sparse spicules are scattered through the remainder of the test although in smaller colonies they sometimes are evenly scattered throughout. Spicules have 11–13 conical rays in optical transverse section, with sharply pointed or chisel-shaped and sometimes bifid or trifid tips. From the surface 2 or 3 of the large spicules are seen in the siphonal lining in the centre of each branchial aperture. There is no superficial bladder cell layer and the surface of the colony is granular and raspy to the touch.

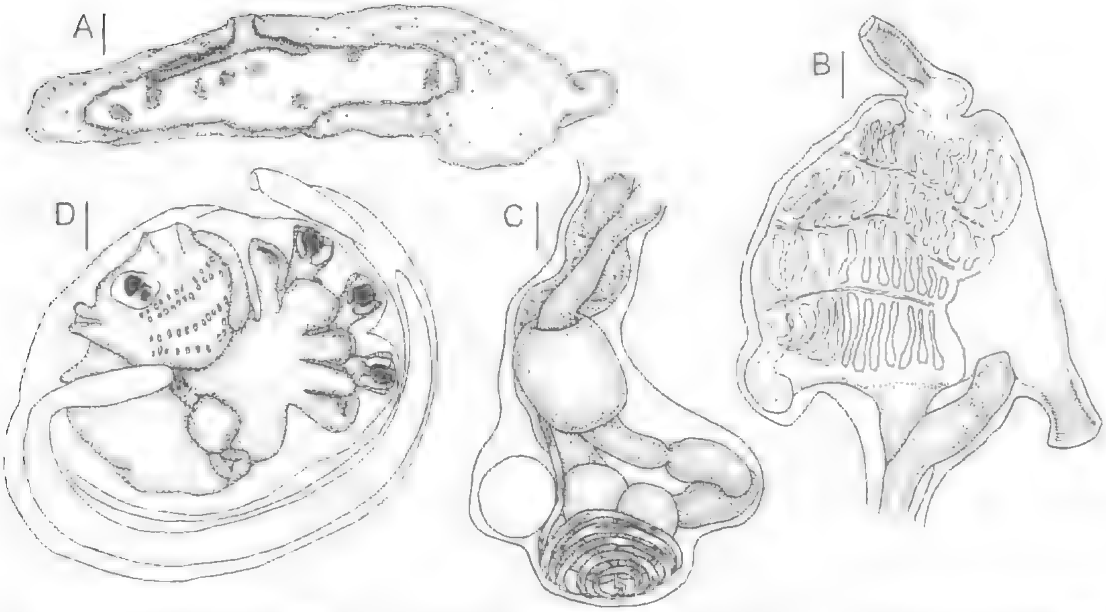


FIG. 21. *Leptoclinides cuspidatus* (A,C,D QM G300956; B, QM G302893) – A, vertical section through a common cloacal aperture; B, thorax; C, abdomen; D, larva . Scales: A, 1.0mm; B–D, 0.1mm.

The type material is said to have been blue marbled with white in preservative, as are all the newly recorded Australian colonies which in life are said to have been dark blue-black. However, the newly recorded colonies from the Philippines are predominantly orange in life with black pigment, sometimes seen through the common cloacal aperture (QM G302893) or in patches of varying size on the surface (QM G300939).

ZOOIDS. Zooids cannot be removed from the test and were examined in handcut, decalcified, and cleared sections. They are large, and often the whole abdomen is folded up against the thorax. Branchial apertures have 6 shallow lobes around the rim. Lobes or papillae were not detected on the atrial aperture although it was not possible to remove it entire from the colony. A large, circular, plate-like lateral organ to 0.2mm diameter is on each side of the base of the atrial siphon. The branchial sac has about 16 stigmata in the anterior row, reducing to about 14 in the last row.

At the base of the relatively long oesophagus the narrow gut loop is bent back at right angles to the proximal part of the loop (the oesophageal neck). The distal part of the gut loop also is bent up slightly. The duodenum is long, wide and expanded distally and the posterior stomach expands to its junction with the wide rectum, where there is an elbow. A constriction about one-third of the way up the rectum is surrounded by glandular tubules.

In the syntypes (ZMA TU440.1, TU440.2) and in the Western Australia colony (collected in August), zooids are sexually mature, with 5 testis follicles in a single tight ring, with the vas deferens making 6 coils around them. Larvae, present in the basal test, are of moderate size, the trunk being 0.75mm long. They have 2 or 3 lateral ampullae along each side of the 3 adhesive organs, and a large median dorsal and median ventral ampulla, respectively, curve around the base of the stalks of the ventral and dorsal adhesive organs.

REMARKS. Characteristic of the species are its raspy surface, large spicules confined to surface and basal layers, dark pigment either mixed with surface spicules or forming a layer beneath them and also lining the posterior abdominal common cloacal cavities, terminal or evenly spaced, slightly protuberant common cloacal apertures, large zooids with 14–16 stigmata and 6 coils of the vas deferens. The newly recorded colonies from the Philippines (QM G302893, G300939) are believed to be conspecific although they are a different colour.

L. apertus (Monniot, 1989) has similar characters to the present species, including two different colony forms, viz, either encrusting or

lobed, and it has a similar range of colours. However, *L. apertus* differs in having 9 (rather than 6) coils of the vas deferens and smaller larvae.

The species is distinguished from *L. brandi* by its black pigment, differently shaped stigmata, the bent distal part of the gut loop, 6 (rather than 5) coils of the vas deferens, absence of a brood pouch, and fewer lateral ampullae in the larval trunk. *L. marsupialis* (Monniot, 1989), which has similar spicules and pigmentation to the present species, also is distinguished by its brood pouch, fusiform stigmata and fewer coils of the vas deferens.

L. oscitans (Monniot & Monniot, 1996) has most reported characters in common with the present species, viz. the surface layer of large spicules with possibly 11–13 rays (with chisel-shaped tips) in optical transverse section, the same dark pigment in branched and fusiform bodies, 14 stigmata per row, 6 coils of the vas deferens, and a similar larva. The distorted atrial aperture probably does not constitute a specific character but may be the result of narcotisation or mutilation associated with removing these zooids from the test.

Like the present species, *L. lissus* Hastings, 1931 lacks a bladder cell layer, and has stellate spicules in the surface layer of test and 3 groups of 2 or 3 spicules in the branchial siphon. However, unlike the present species, the spicules are only 0.04–0.05mm in diameter. The orange colonies of *L. sulawesii* have numerous elevated common cloacal apertures, like the present species, but they lack the black pigment and have smaller spicules.

Leptoclinides dubius (Sluiter, 1909)
(Figs 22, 161A; Pl. 2E–H)

Polysyncraton dubium Sluiter, 1909: 69. Van Name, 1918: 158 (part, colonies from stations D5145, D5174).
Leptoclinides dubius: Michaelsen, 1930: 507 f. typicus. Kott, 1962: 288 f. typicus; 1998: 86. Millar, 1975: 238. Monniot, 1989: 681.
Not *Leptoclinides dubius*: Tokioka, 1952: 94 (< *L. durus* sp. nov.). ? Monniot & Monniot, 1996: 176.

NEW RECORDS. Western Australia (Houtman's Abrolhos, WAM833.83, QM GH2112). Queensland (Capricorn Group, QM GH809, GH887, GH1356, GH1363, GH1365, G300895, G300906, G300908-10, G300913-8, G301516, G301932, G301955, G302106, G302135, G302165, G302220, G302433, G302530, G302561, G302569, G302965, G302997, G308038, G308051, G308092, G308102, G308192, G308232-6, G308239, G308258, G308272, G308497; Swain Reefs, QM G305410, G305490, G305761, G308358, G308376; Whitsunday Is., QM G302936; Abbot Point, 30km NW Bowen, QM G302139; Lizard I., QM G302196, G302231-3, G302237).

PREVIOUSLY RECORDED. Indonesia (lectotype ZMA TU1275, paralectotypes TU834.1, TU834.2 Sluiter, 1909). Philippines (USNM 5900, 5901 Van Name, 1918; Millar, 1975). New Caledonia (Monniot, 1989).

COLONY. Colonies are encrusting sheets with the surface raised into low domes, long curved ridges, or conical protuberances with terminal common cloacal apertures. These elevations sometimes are only around the outer margin of the colony, but sometimes the whole surface is raised into small protuberances. Crowded spicules are in a thin layer at the surface of the colony, and a spicule-free superficial layer of bladder cells was not detected. Spicules usually are absent around the rim of the cloacal apertures. They are sparse in the remainder of the test, although an even layer lines the cloacal cavity and another layer is present on the base of the colony. Sometimes (QM G305410), the superficial layer of test contains opaque clumps of spicules of irregular size, shape and distribution continuous with an even layer just beneath the surface. Branchial apertures are conspicuous on the surface of the colony, with a layer of spicules in the longitudinally grooved siphonal lining appearing from the surface as a margin of spicules outlining the sharply stellate aperture and leaving a spicule-free spot alternating with the 6 grooves.

Capacious posterior abdominal common cloacal cavities are beneath the raised surface domes. The atrial apertures open into canals that penetrate the zooid-bearing layer of test rather than directly into the large cloacal cavities beneath the zooids. Cloacal apertures are large, although they are not permanently open. They are often irregular, sometimes being long slits rather than circular openings. They are sometimes relatively few and irregularly distributed, sometimes only at one end of the colony.

Spicules have up to 17 rays in optical transverse section and are relatively small (up to about 0.032mm in diameter). A few larger spicules (to 0.04mm) have only about 9 conical rays in optical transverse section. Many of the spicules have long rod-like, round-tipped rays (rather like the spines of a slate-pencil urchin), but in others the rays are slender, pointed and almost fusiform, and others have blunt-tipped or short conical rays. Only smaller spicules are globular.

Colours recorded for living colonies are. ferruginous[R] or rufous[R] test with dragons

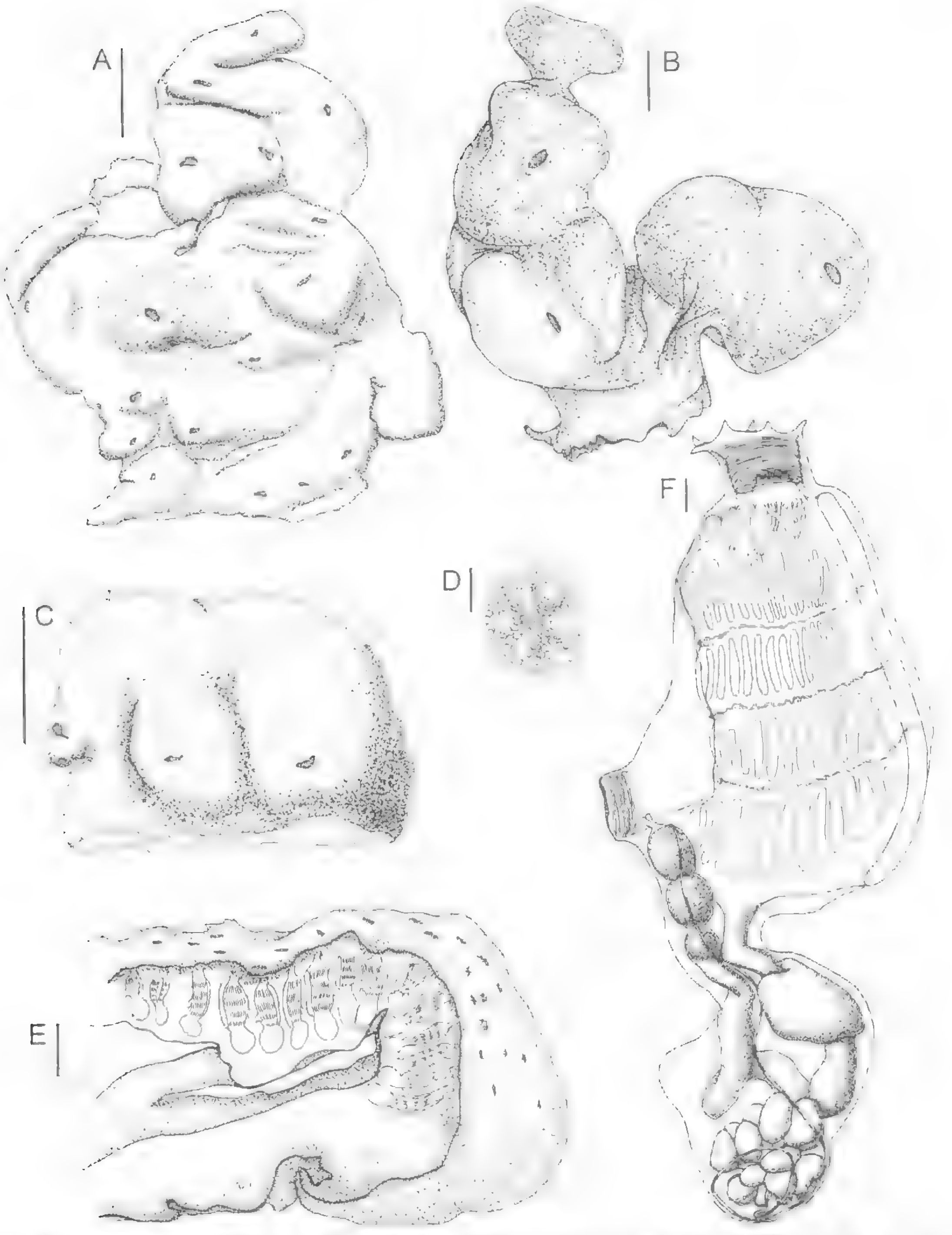


FIG. 22. *Leptoclinides dubius* (A, QM G302106; B,E, QM G305490; C,D, QM GH887; F, QM G302196) A–C, portions of colonies showing terminal common cloacal apertures; D, a branchial aperture showing arrangement of spicules lining the aperture; E, semidiagrammatic vertical section through colony showing large posterior common cloacal cavity, F, zooid showing false siphon at base of the branchial siphon, ventrally flexed gut loop, and grape-like cluster of testis follicles. Scales: A–C, 1.0cm; D,F, 0.1mm; E, 1.0mm.

blood-red[R] zooids, orange chrome[R] with scarlet[R] zooids, orange with dark zooids, rose purple[R] with black zooids, heliotrope purple[R] with orange zooids, olive grey[R] with chocolate[R] zooids and chocolate[R] in and around cloacal apertures, lilac grey[R], dahlia purple[R], grey, pansy purple[R], grey-white-veiled, light and dark grey[R], grey-brown[R], mummy brown[R] and grey-orange[R]. In a few colonies (e.g. QM G302561) the test is white, zooids are vinaceous[R] to rufous[R], and eggs are deep orange. Generally rims of the cloacal apertures are affected by the absence of spicules. They are brown or black — darker than the rest of the surface, but in other specimens they are orange. The openings themselves are dark inside, owing to pigment in the internal test. Magnification of the surface shows that the colours are the result of irregular black, brown and yellow pigment cells below and sometimes mixed with the white spicules. In preservative some of the colonies become brown/orange, and the preservative is stained a brown-orange colour to clear lemon. In some preserved specimens there are streaks and oval patches of green orange pigment amongst the spicules in the surface test. Occasionally patches of green *Prochloron* are on the surface of the colony (QM GH887).

ZOOIDS. Zooids are relatively large (about 3mm long). A short atrial siphon, with a smooth-rimmed aperture projects posteriorly from the postero-dorsal corner of the thorax. Fine longitudinal muscles (about 12) are in the thoracic body wall. Circular muscles surround both branchial and atrial siphons. The branchial aperture has 6 distinct pointed lobes around its rim and is on a robust siphon with a pronounced velum at its base forming a forward projecting false siphon. The ring of branchial tentacles is posterior to the velum. A short neural duct from beneath (ventral to) the ganglion curves to open directly into the pharynx behind the tentacles. Stigmata are long and narrow, and arranged in 4 rows of about 14 per row.

The gut loop is long, and its post-pyloric part is bent ventrally and up against the anterior part of the loop, to form a secondary loop. The stomach is almost spherical and smooth, and the duodenum long and bulbous with a distal expansion. A small oval posterior stomach is in the pole of the gut loop. The rectum is wide at its proximal end and has the usual constriction about halfway along its length where the gastric gland tubules surround it. A spherical mass of what may be glandular material is in the gut loop. Gonads are posterior to and up against the ventrally flexed part of the gut loop. The testis is large and spherical with a 3-dimensional mass of up to 20 follicles converging into the centre. The vas deferens emerges from the centre of the spherical testis, and coils only once or forms an S on its outer or posterior surface before extending anteriorly to open with the anus in the base of the atrial siphon. The direction of the coil is either clockwise or anticlockwise and the S is formed by changing direction from clockwise to anticlockwise (or the reverse) after emerging from the testis. The ovary is over the centre of the outside of the testis at the proximal end of the vas deferens. Testes are mature in specimens collected in January, April and November.

Embryos were present in a specimen from the southern end of the Great Barrier Reef taken in March (QM G300914). Larvae are large with a trunk about 1.2mm long and the tail wound about three quarters of the way around it, 3 adhesive organs and 6 pairs of lateral ampullae. Larvae recorded by Monniot (1989) and Millar (1975) have trunks 1.4mm and 1.0mm long respectively, and 6 ampullae per side.

REMARKS. Although other species have similar colonies and colonial systems, this one is distinguished by its single layer of spicules at the surface of the colony, the diverse forms of these relatively small spicules, stellate branchial apertures outlined in spicules, absence of a superficial layer of bladder cells, large zooids each with a conspicuous false siphon at the base of the branchial siphon, long gut loop with its distal part bent up to form a double loop, long bulbous duodenum, spherical testis with grape-like cluster of follicles converging from the outside into the centre, relatively few vas deferens coils, and large larvae with 6 pairs of lateral ampullae.

All species of the *dubius* group lack a superficial bladder cell layer, have a similar false branchial siphon, double gut loop, grape-like spherical mass of testis follicles, short vas deferens and large larva. They are distinguished from one another mainly by the form of the spicules. *L. levitatus* and *L. multilobatus* most closely resemble the present species. The zooids and spicules of *L. dubius* are larger than those of *L. multilobatus*, the spicules have more numerous rays than those of *L. levitatus*, and are more variable in form than in *L. durus* and *L. kingi* (which only have spicules with pointed conical rays). *L. echinus* has less variable

spicules than the present species, all with long, pointed rays.

Millar (1975) described specimens with algal cells in the common cloaca. Although *Prochloron* is found on the surface of this (see also Monniot, 1989) and other *Leptoclinides* species, Millar's is the only report of this symbiont in the cloacal cavity. It is not an obligate relationship, however, and there are many specimens without *Prochloron*. Obligate symbioses with *Prochloron* have not been recorded from this genus. Commensal gastropods and crustaceans are embedded in the basal test.

Certain of the specimens assigned to this species by Van Name (1918) were found to be incorrectly assigned. Thus USNM 5899 (D5109) is *Lissoclinum patella* (Kott, 1980, 1981, 1982 synonymy and below); USNM 6033 (D5139) is a specimen of an undescribed species with a surface layer of bladder cells, about 10 male follicles in a 3-dimensional mass and 6 coils of the vas deferens; USNM 6032 (D5150) may be a specimen of *L. rufus* with dark pigment cells in a thick superficial layer of bladder cells over a layer of relatively large (0.06mm diameter) spicules. Specimens USNM 5996 (D5555) and one from Station D5136 were not located. Van Name (1918) also proposed *Leptoclinides margaritiferae* (Herdman, 1906) from Sri Lanka as a possible synonym of the present species. This is not resolved.

Although it has a grape-like cluster of eggs and one coil of the vas deferens, *Leptoclinides dubius*: Monniot & Monniot, 1996 from Indonesia has spicules numerous only in the basal part of the colony and consequently does not belong to the present species which has spicules crowded at the surface. It could be a synonym of *L. kingi*. Nevertheless, as other characteristics of the colonies as well as the spicules, zooids and larvae are not described, it is not possible to confirm the identity of the material from the published description with any confidence.

Leptoclinides durus sp. nov.
(Figs 23, 161B; Pl. 3A,B)

Leptoclinides dubius: Tokioka, 1952: 94.

TYPE LOCALITY. Queensland (Heron I. on coral rubble, coll. P. Kott 30.9.79, holotype QM G302350; Heron I. 10m, coll. D. Watters 27.10.92, paratype QM G300893. Swain Reefs, 6m, coll. P. Saenger 22-106 18.1.84, paratype QM G302045).

FURTHER RECORDS. Western Australia (Bonaparte Archipelago, QM G300933, G302888, G302929); Queensland (Heron I., QM G308261; Swain Reefs, QM G305368, G305377, G305555, G305806, G308364, G308385, G308411; NW of Penrith, QM G300975; Palm I., QM G300957; Hazlewood I., QM G302947; Hinchinbrook I., QM G302868; Deloraine I., QM GH5368; Dingo Reef, QM GH5784). Arafura Sea (Tokioka, 1952). Micronesia (Monniot & Monniot, 1996).

The species does not appear to be common in waters less than 6m deep.

COLONY. Colonies (up to 20cm in maximum dimension) are flat, rigid, encrusting sheets, with an even, hard usually smooth surface but sometimes with minute spicule-filled papillae making it raspy. Common cloacal apertures are large and conspicuous, sessile with frilled lips, or on protuberant chimney-like elevations, the only conspicuous elevations on the surface, usually around the margins of the colony about 1–2cm apart. A single layer of spicules in the test lining the branchial siphons appears from the surface as a line of spicules around the edge of the stellate aperture. Outside the aperture a narrow spicule-free band appears as a dot in each lobe of the stellate aperture. Five short rows of 2–4 spicules radiate around each of the atrial openings into the cloacal cavities. Common cloacal apertures open into extensive posterior abdominal spaces interrupted by test connectives attaching clumps of zooids in the surface layer of test to the basal layer. Spicules are crowded throughout the test, and the whole colony is hard, rigid and brittle. Spicules are particularly crowded in a thin, hard basal layer which is rippled in preserved specimens. This very hard basal layer of test may be associated with the ease with which these colonies are removed from the substrate. The ripples on the base are not a mould of the substrate however.

Small (to 0.0375mm diameter) spicules mostly have pointed conical rays of various lengths, 9–11 in optical transverse section. Only very few are globular with flat-ended rays.

The colour in life usually is intense. Colonies are purple or orange, chinese orange[R], chrome yellow[R], rufous or burnt carmine[R] with dragon's blood[R], lake red[R], rufous brown[R], or crimson[R] zooids. Colonies also have been described as liver brown, thick purply-yellow, brown, pink, purple, brown/red and reddish-purple. The colour is confined to the surface and contrasts with the stark white of the crowded spicules which are exposed in a band around the common cloacal apertures and are seen from the surface lining the rigid common cloacal canals. Orange pigment sometimes persists in the surface of the test just above the spicules and in the zooids.

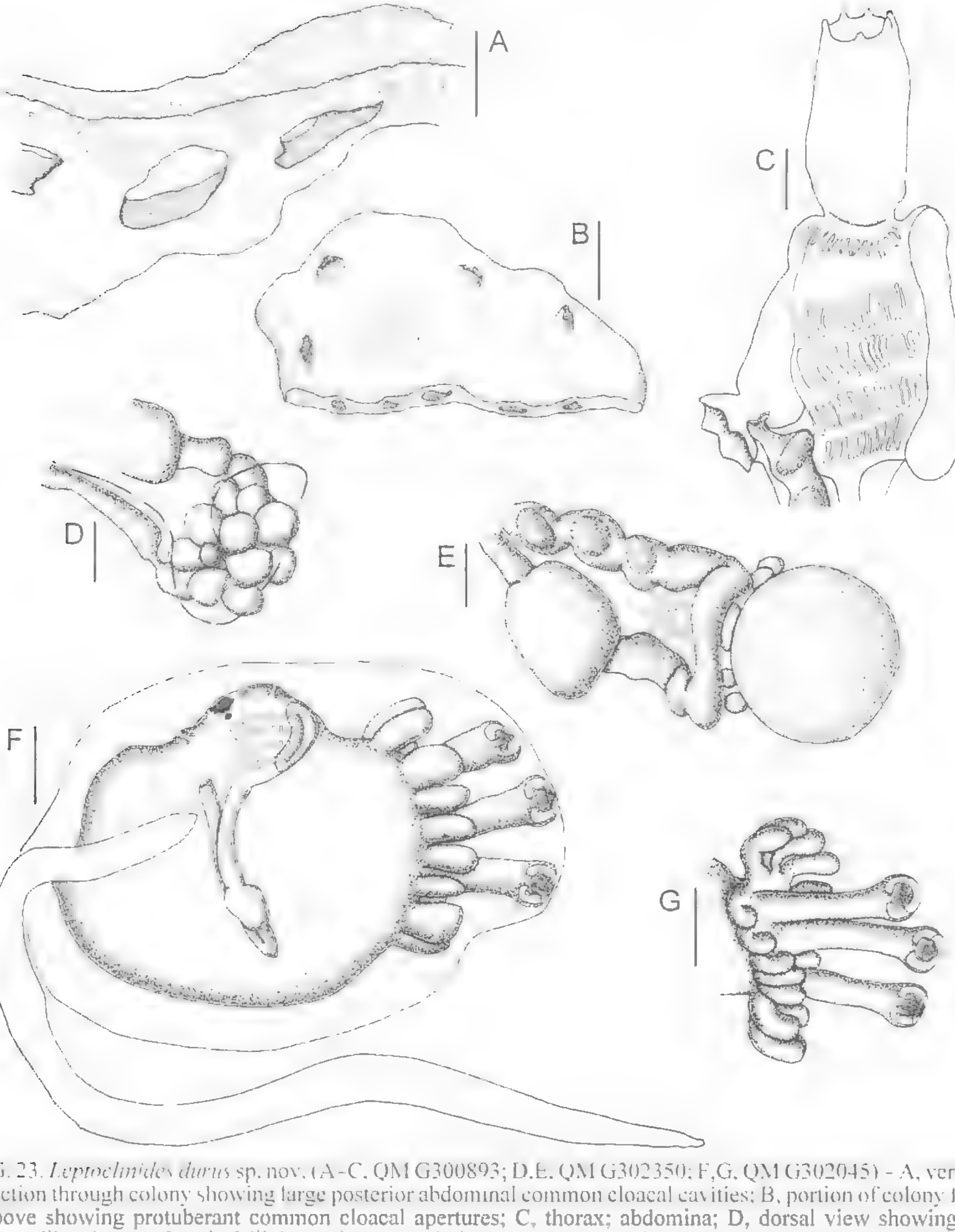


FIG. 23. *Leptoclinides durus* sp. nov. (A–C, QM G300893; D,E, QM G302350; F,G, QM G302045) - A, vertical section through colony showing large posterior abdominal common cloacal cavities; B, portion of colony from above showing protuberant common cloacal apertures; C, thorax; abdomina; D, dorsal view showing the grape-like cluster of testis follicles and E, ventral view showing ventrally flexed gut loop and a large egg; F, larva; G, adhesive array at anterior end of larval trunk. Scales: A, 1.0mm; B, 1.0cm; C–G, 0.2mm.

Specimens from the Whitsunday Is (QM GH5368, G302947) have patches of *Prochloron* on the surface.

ZOOIDS. Zooids are about 2mm to the end of the gut loop. However gonads lie behind the gut loop, at the posterior end of the body, and when mature they extend the zooid's length appreciably. The branchial siphon is conspicuous, long and muscular, and cylindrical or funnel-shaped. Circular muscles are especially crowded around

its basal part. A narrow velum is present at the base of the branchial siphon, but a false siphon, as in other species of the *dubius* group was not detected. Six small pointed papillae, the homologues of branchial lobes, are present around the rim of the branchial opening. The short atrial siphon is also funnel-shaped, posteriorly directed and with a smooth rim. A large lateral organ is opposite the third row of stigmata. An extensive imperforate part of the pharynx is anterior to the perforated area. Middle rows of the branchial sac each have 14 stigmata and the anterior and posterior rows have 12 or 13.

The gut loop is long, with the usual duodenum, posterior stomach and wide proximal part of the rectum. The post-pyloric part of the gut loop is bent up ventrally against the pyloric part to form a double loop. The rectum narrows conspicuously in the elbow of the bend where it is surrounded by a mass of gastric tubules. A curved mass of vesicles is in the ventral curve of the pole of the gut loop and the testis is on the other (dorsal) side of the recurved part, at the posterior end of the zooid. The testis, consisting of a 3-dimensional mass of 9–12 follicles, has the vas deferens loosely wound around it twice only . A single egg is in the middle of the outer surface of the testis and when well developed is orange and crowds the testis against the gut loop.

Embryos are present in the basal test of specimens from the Swain Reefs (QM G302045) collected in January and off Bonaparte Archipelago (QM G302888) in August. Tailed larvae are present just below the surface test of this specimen, and some, with regressing tail, are being liberated through perforations in the surface test. The larvae are large, with the trunk 1.5mm long. Adhesive organs are on long, cylindrical stalks. Eight rounded ectodermal ampullae are on each side of the 3 antero-median adhesive organs.

REMARKS. Spicules are similar to, and in the same size range as, those of *L. kingi*, generally having short conical pointed rays. They differ from those of *L. dubius* in being less diverse (lacking the spicules with long, narrow, blunt-ended as well as pointed rays found in *L. dubius*). As in other species of the *dubius* group, the small spicules outline the margin of the stellate branchial apertures, the distal part of the gut loop is bent up ventrally, a curved mass of vesicles is in the gut loop, the testis follicles are grouped into a 3-dimensional mass, the ovum is on the outside of the testis, and the vas deferens makes only a few turns around the testis. Generally, the larva also is like that of others in the *dubius* group, being large (>1mm), with numerous ampullae, although it is larger and has even more numerous ampullae than other species. The principal distinction from *L. dubius* and other members of the *dubius* group is the even, hard colony surface, spicules crowded throughout the colony, and the absence of a wide branchial velum and false siphon.

The specimen from the Arafura Sea (Tokioka, 1952), with spicules of characteristic form crowded throughout the test, is conspecific with the present species rather than *L. dubius*. *L. dubius*: Monniot, 1989 has a larval trunk 1.5mm long, like the present species. However it otherwise resembles *L. dubius*, especially in having its spicules confined to a surface and basal layer.

Leptoclinides uniorbis Monniot & Monniot, 1996, has a hard orange colony with ripple marks on the base, spicules to 0.04mm diameter, 2 coils of the vas deferens around a compact rosette of 6–8 testis follicles and 18 stigmata are in the anterior row. The atrial cavity is said to be limited, but as stigmata presumably open into it, it is not clear how the atrial cavity is restricted in *L. uniorbis*, unless this refers to an extensive prestigmatal unperforated area in the branchial sac, as in the present species. The spicules of *L. uniorbis* constitute a distinction, having more rays, some with rod-like, flat-tipped rays as well as globular ones.

Leptoclinides echinus sp. nov.
(Figs 24, 160H; Pl. 3C)

TYPE LOCALITY. Western Australia (8.5 n miles NWN Port Hedland 20°13'S 118°28'E, 18m, coll. J. Fromont statn 50 RV Soela 4A/82.13, holotype WAM865.83(1) QM GH2121); Dampier Archipelago, western end of Lewis I., 12m, coll. AIMS Bioactivity Group Q66C 1612 1.9.88, paratype QM G302871).

COLONY. Both colonies are large and complex — the complexity possibly being a result of growth. They have a gelatinous appearance (owing to the rather sparse concentration of spicules in the surface) and consist of extensive convoluted sheets, forming irregular, lobed masses. Zooids open on both sides of the lobes and lamellae where basal surfaces are folded together and adhere to one another. A very extensive posterior abdominal cloacal cavity is crossed by strands of test connecting the basal or central test mass to the outer zooid-bearing layer. In life (see photographed specimen QM

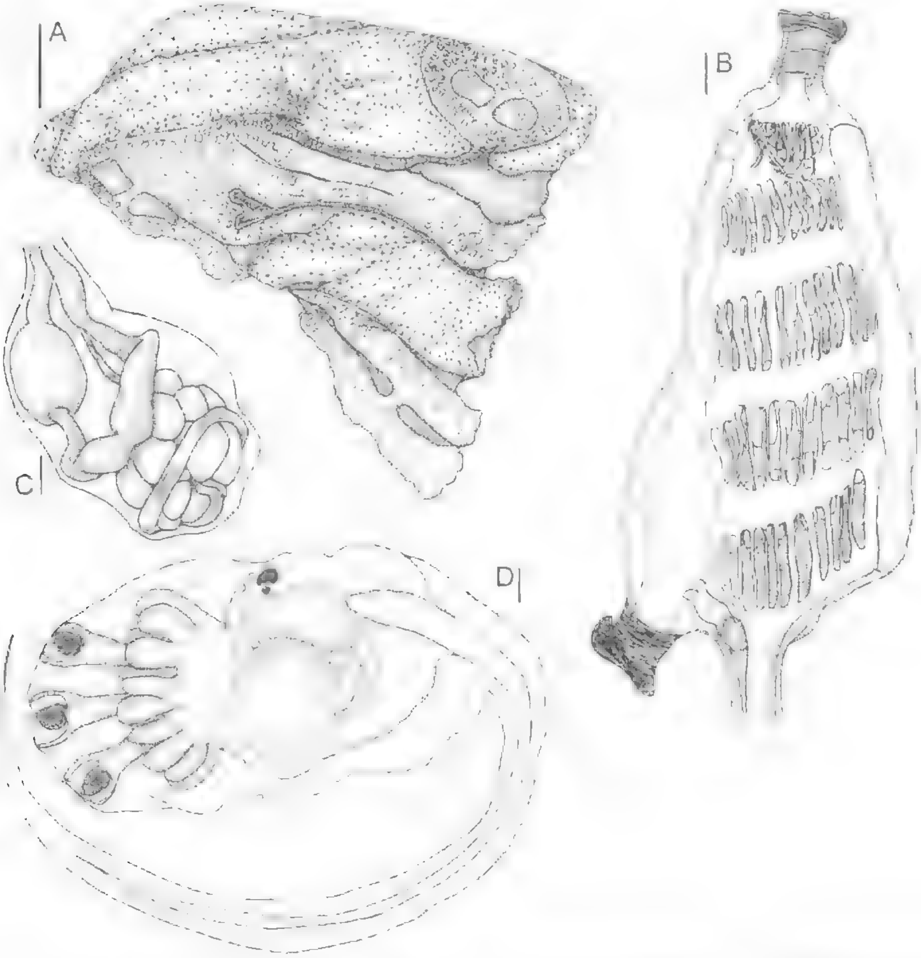


FIG. 24. *Leptoclinides echinus* sp. nov. (A, QM GH2121; B-D QM G302871) – A, vertical section through colony showing complex folding; B, thorax; C, abdomen; D, larva. Scales: A, 10.0cm; B–D, 0.1mm.

G302871) colonies are dark brown with orange rings around groups of branchial apertures.

Spicules are evenly spaced in the surface test. A superficial bladder cell layer is not present. Spicules line the common cloacal cavity although there they are less crowded than in the surface and are only sparse elsewhere. The branchial siphons are lined with spicules, although only occasionally is there a spicule-free area (appearing from the surface as spicule-free spots) around the apertures. Small, (seldom more than 0.03mm in diameter) spicules with 9 to 11 long, pointed rays in optical transverse section, are relatively uniform.

ZOOIDS. Zooids are small. A small false siphon is at the base of the branchial siphon. The branchial aperture has 6 small papilla-like projections around the aperture. The atrial siphon is posteriorly oriented from the postero-dorsal corner of the thorax. Twelve to 14 stigmata are in each row in the branchial sac. The post-pyloric part of the gut loop is bent ventrally and up against the pyloric part to form a secondary loop. Beneath this (at the posterior end of the zooid) is a spherical cluster of about 15 testis follicles. The vas deferens takes an S-shaped course over the outer surface of the testis. The 'bright orange vesicles' observed in the living paratype may be maturing eggs. Larvae are large, with a trunk 1.5mm long and the tail wound only halfway around it. There are four bilobed lateral ampullae along each side of the 3 median adhesive organs. These bifid lateral ampullae in due course subdivide to form 8 finger-like ampullae along each side of the 3 antero-median adhesive organs.

REMARKS. The unique character of this species by which it may be distinguished from others, is the spiky form of the relatively uniform spicules. Otherwise both colony and zooids have the general aspects of the *dubius* group of species — extensive common cloacal cavities, branchial velum in the base of the siphon, double gut loop, spherical cluster of testis follicles and S-shaped course of the vas deferens. The colonies are more complex than others of the group, but it is assumed that this is a result of growth and maturity.

Spicules most resemble those of *L. levitatus* from Rockingham (see below), which also have long spiky rays and a similar colony — relatively thick with a large cloacal cavity separating the surface zooid-bearing layer of test from the thick basal test, and with the spicules mainly in the surface. However the present species has only one type of stellate spicule, those with long, pointed rays, while *L. levitatus* has a variety of ray shapes, more spicule rays and rays of various lengths in a single spicule.

Leptoclinides erinaceus sp. nov.
(Figs 25, 158E)

TYPE LOCALITY. Western Australia (24 n miles NNW Port Hedland 19°57.2'S 118°25.1'E 22-24m, coll. L. Marsh and M.Bezant on RV Soela 25.9.82, holotype WAM128.93).

FURTHER RECORDS. Queensland (Hardy Reef, QM GH5735).

COLONY. The holotype colony is a thin (about 3mm thick) encrusting sheet. Spicules are in a layer at the surface, in moderate concentrations in the upper half of the colony and in a simple, sparse layer on the basal surface, but are almost completely absent from the translucent lower half of the colony, where large, crowded bladder cells can be clearly seen in stained mounted sections. Only restricted cloacal canals are evident in the holotype colony, in which adult thoraces are regressed and juvenile vegetative ones developing. Zooids lie horizontally in the upper half of the colony amongst the spicules, and yellowish embryos (but not tailed larvae) are in the aspicular lower half. In the specimen from Hardy Reef zooids line deep circular primary cloacal canals which extend into posterior abdominal spaces.

Spicules are large (to 0.15mm diameter) with 13–15 relatively long conical rays with pointed and chisel-shaped tips. The ray length/spicule diameter ratio is about 0.3.

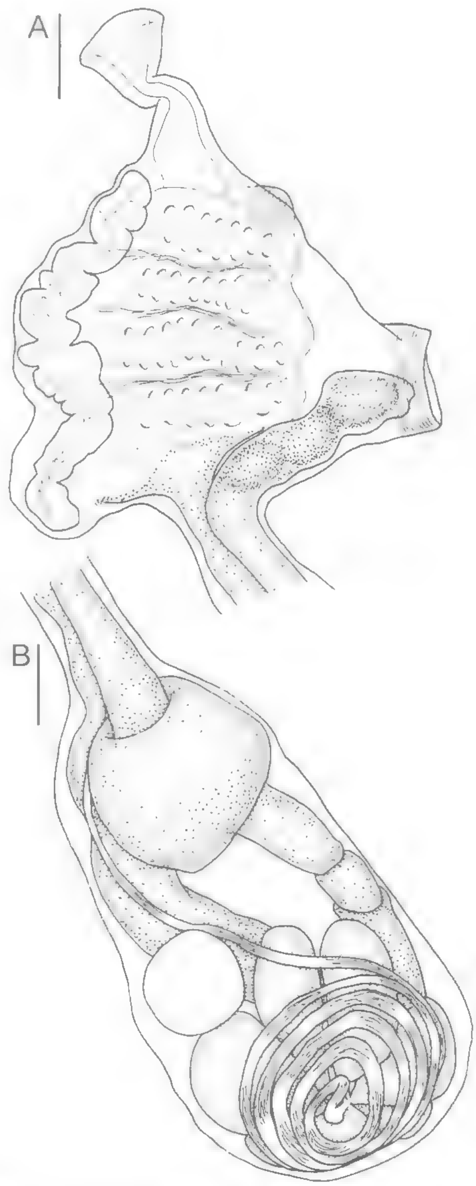


FIG. 25. *Leptoclinides erinaceus* sp. nov. (QM GH5735) – A, thorax. B, abdomen. Scales: 0.1mm.

A deck photograph of the Hardy Reef specimen shows it as black although the field notes report it as red/purple mottled (McCauley et al., 1993: Q66B2198, III: 5).

ZOOIDS. Juvenile vegetative thoraces, and mature abdomina with well developed gonads are present in the holotype colony. The abdomina are about 0.6mm long and it is probable that the total length of an entire zooid would be greater than 1.0mm. The juvenile thoraces have a posteriorly

directed cylindrical siphon with a broad sphincter and 4 rows of stigmata with about 10 per row.

The gut loop is relatively long but does not form a secondary loop. The testis is divided into 7 follicles and the vas deferens spirals 6 times around them.

REMARKS. The large spicules with numerous sharply pointed rays resemble those of *L. brandi*, but are smaller with more, longer and more sharply pointed as well as chisel-shaped rays. Further, embryos develop in the basal layers of test while those of *L. brandi* are in a brood pouch attached to the posterior end of the thorax. *L. magnistellus* from Tasmania has similar, albeit significantly larger spicules, while *L. cavernosus* has smaller ones with more rays. *L. maculatus* has similar spicules to the present species but they are smaller (to 0.07mm diameter) and have fewer (9–11) rays. *L. rigidus* and *L. aciculus* also have similar but smaller spicules with fewer rays, but the former has a distinctive superficial bladder cell layer and the latter more vas deferens coils.

Leptoclinides exiguus sp. nov.
(Figs 26, 159H; Pl. 3D)

Leptoclinides rufus: Kott, 1975: 9.

TYPE LOCALITY. South Australia (Spencer Gulf Point Turton jetty, 5m, coll. AIMS Bioactivity Group 4.2.89, holotype QM G300947). Victoria (Flinders Pier, 5m, coll. N. Coleman 15.6.77 AMPI 203, paratype QM G10166).

FURTHER RECORDS. South Australia (Top Gallant I., QM GH1290; Point Turton, SAM E2624; Rapid Bay, E2660; Flinders I., QM GH1289; Spencer Gulf, QM G301615; Ward I., QM GH1286, GH1318; Kangaroo I., QM G302925). Victoria (ESE side Gabo I., AM Y2287; Western Port, QM G300925, G300994, MV F68745, F68763, QM G308569).

COLONY. Colonies are thin (3–4mm) but rather fleshy, tough and extensive sheets usually with the surface marked into a grey to black marbled pattern or network of narrow depressions (containing double rows of branchial openings) surrounding small solid oval or circular raised areas of solid test about 2mm in diameter. Sometimes spicules are mixed in with a thin superficial layer of bladder cells (QM GH1286). Inconspicuous common cloacal apertures are evenly distributed, about 8mm apart in the depressed areas, at the junction of canals. Beneath the surface depressions, the common cloacal canals are usually oesophageal, but sometimes are deeper. Zooids are embedded around the periphery of the solid test cores, their atrial apertures directed out to the cloacal canals.

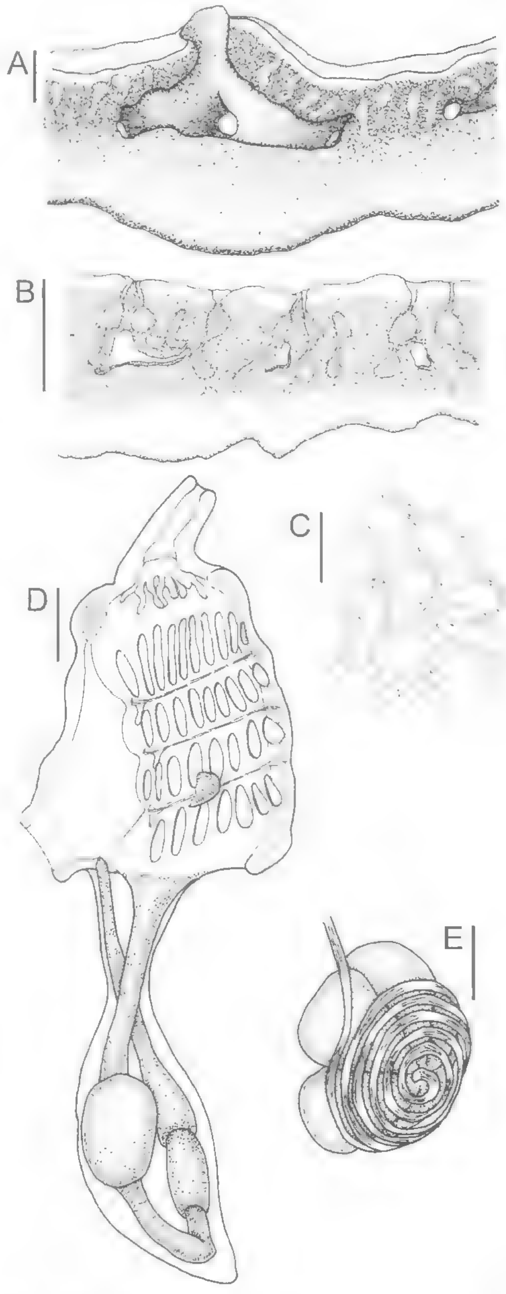


FIG. 26. *Leptoclinides exiguus* sp. nov. (A–C,E, QM G301615; D, QM G300994) – A, semidiagrammatic vertical sections through colony, showing superficial bladder cell layer and deep common cloacal chamber beneath common cloacal aperture; B, zooids lining each side of deep primary common cloacal canals; C, part of surface with branchial apertures along each side of the common cloacal canals that surround the raised zooid-free areas of test forming a mosaic on the surface; D, zooid; E, testis. Scales: A,B, 1.0mm; C, 2.0mm; D,E, 0.1mm.

In 2 specimens from Western Port (QM G300925, G300994) in which zooids are not sexually mature, the cloacal spaces are not developed and the upper surfaces are smooth and even without the depressions that usually develop over the deep primary canals.

Spicules are in 3 small clumps or rows converging in the centre of each branchial aperture. Spicules are evenly scattered and moderately crowded in the upper half of the colony beneath the bladder cell layer around the zooids but are sparse, or absent from, the basal one-third to half of the colony, although a sparse layer is present on the lower surface. They are relatively large, occasionally reaching 0.08mm in diameter, although generally the largest are only 0.05mm. They have 9–11 conical rays with chisel-shaped tips in optical transverse section.

In preserved specimens dark grey to black pigmented depressions in the surface result from spherical to irregular dark pigment particles around the zooids. Raised areas are white — where a greater depth of spicules is in the zooid-free solid test. Preservative stains green, reservoirs of green pigment being in the basal test. Living specimens are reported to have had a green matrix with orange zooids or to have been white with black zooids (QM GH1289) or dark purple blue (QM G300994) or orange (QM GH1318). The reference to 'zooids' in this context is probably a misinterpretation of the pigment pattern. Specimens from Flinders Pier were black and orange in life (QM G10166, G308569).

ZOOIDS. Zooids are relatively small (about 1.5mm long), and not readily removed from the test. Forward projecting columnar epidermal cells are conspicuous on the anterior thoracic wall. Branchial siphons are long, the rim without conspicuous branchial lobes. The atrial siphon is directed posteriorly from the postero-dorsal corner of the thorax. A round lateral organ is in the middle of each side of the thorax, level with the base of the atrial siphon. Ten stigmata are in the anterior row, 9 in the second, 8 in the third and 7 in the posterior row. The gut loop is rounded and open. The oesophagus is relatively short, the stomach almost spherical, the duodenum also relatively short, and the posterior stomach (in the pole of the loop) small and rounded. The distal part of the rectum is a narrow tube. The post-pyloric part of the gut loop is flexed ventrally over the testis, which consists of 5 or 6 follicles crowded into a circle (but not in a single ring), with an outer cap of 6 coils of the vas deferens. Tailed embryos occur in the basal test of a colony collected in March (QM GH1318). Although the otolith and ocellus are well-formed, no other organs were distinguished in the small trunk (0.45mm long).

REMARKS. The species is distinguished from other temperate *Leptoclinides* spp. with zooids tightly attached to the test (e.g. *L. compactus*, *L. maculatus* and *L. variegatus*) by its double rows of zooids opening into the network of darkly pigmented depressions in the surface test. Like *L. variegatus* it has larger spicules than *L. compactus* and *L. maculatus*. Also, in *L. maculatus* some spicule rays have truncated tips, black pigment spots usually regularly distributed in the thin superficial layer of bladder cells over the primary common cloacal canals and 8 rather than 5 coils of the vas deferens. *L. variegatus* has larger spicules with more rays and a smooth colony surface. Usually it can be distinguished from the present species by the position of its cloacal apertures found particularly near the margins of the colony (rather than being scattered over the surface). *L. aciculus* has the same colony form as the present species but its spicules are larger with long rays. The tropical *L. rigidus* has similar spicules but its cloacal systems are more extensive and it lacks the grey meshwork in the surface. *L. umbrosus*, has dark pigment but lacks the colour pattern of the present species, and has larger spicules with more and shorter rays.

Leptoclinides fungiformis Kott, 1972
(Fig. 27)

Leptoclinides fungiformis Kott, 1972b: 180; 1998: 86.

NEW RECORDS. ? South Australia (Investigator Strait, MV F68815, F68820).

PREVIOUSLY RECORDED. South Australia (Pearson I. – SAM E911 syntypes Kott, 1972b).

COLONY. Colonies are stalked heads, up to 7cm high, of which the head is about 2cm and the thick, transversely wrinkled stalk is 5cm. Basally, the stalk expands slightly into a holdfast. The head is slightly laterally flattened, wider at the top and narrowing to the stalk. One or 2 large common cloacal apertures are approximately in the centre of the upper free surface of the head. The outer surface of the colony is firm and smooth, but although it is firm the test is not tough. The position of the branchial apertures on the surface of these colonies is marked by a small dimple. The crowded spicules obscure the arrangement of the zooids. A superficial layer of bladder cells was not detected, and spicules are crowded in the surface. Spicules are less crowded

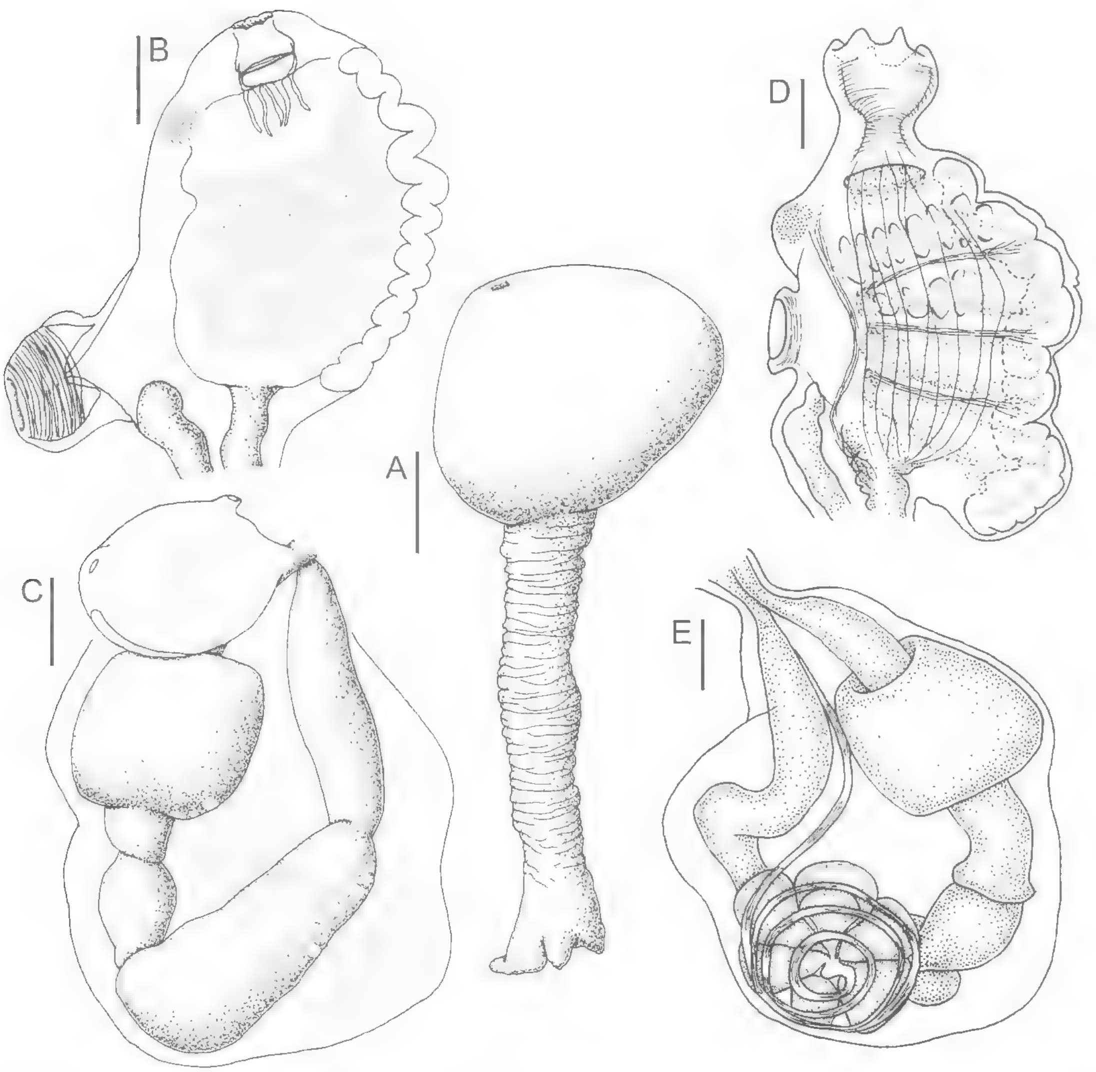


FIG. 27. *Leptoclinides fungiformis* (SAM E911) – A, colony; B, zooid; C, gut loop and oesophageal bud. ? *L. fungiformis* (MV F68820) – D, thorax; E, abdomen. Scales: A, 1.0cm; B–E, 0.1mm.

but evenly spaced around the zooids and in the central test of both the stalk and the head. They are small (to 0.02mm in diameter), with numerous (about 15) short, conical, but sometimes flat-ended rays in optical transverse section. A few have only about 7 conical rays in optical transverse section. Shallow, but extensive, posterior abdominal common cloacal cavities separate the central test from the surface layer around the head of the colony, and secondary canals from cavities at oesophageal level open into them. Longitudinal spaces in the stalk may be vascular, or at least partially the result of shrinkage of the test.

ZOOIDS. In the syntype material zooids are in the vegetative phase, with thoracic and abdominal buds. The thorax and abdomen are of about equal length. The branchial apertures on short cylindrical siphons are smooth-rimmed. The posteriorly directed atrial aperture is on a conspicuous siphon projecting from the postero-dorsal corner of the thorax. Its distal part is bulbous, with a wide, thick sphincter around it. A velum in the base of the atrial siphon projects into the siphon as a conical false siphon. Some fine longitudinal muscle bands are on the thorax. Thoracic buds from the oesophageal neck have 4 rows of about 8 stigmata but they could not be

counted accurately. The gut forms a fairly open loop, flexed ventrally in front of the stomach. Kott (1972b) reported a single male follicle, confirmed by Monniot (1989). Re-examination of the syntype material has not confirmed this, and the structure of the testis is uncertain. A single egg is present in the test behind each zooid. Larvae are not known for this species.

REMARKS. The colony resembles that of the sympatric *L. volvus* (also occurring in South Australia). However, *L. volvus* lacks a posterior abdominal cloacal cavity and has double rows of zooids surrounding protuberant zooid-free areas of test, a superficial bladder cell layer, a short, laterally directed atrial siphon, a distinct branchial siphon, short conical spicule rays, and spicules present throughout the colony including the stalk.

The specimens from Investigator Strait doubtfully assigned to this species are stalked, with spicules in clouds at zooid level and in the central test. The branchial siphon has pointed lobes, the atrial siphon is short at mid thorax level, 6 testis follicles are arranged in a circle and 4 coils of the vas deferens surround them. More material is needed to establish whether the differences (principally in the thorax) from the syntypes are significant, or are merely associated with the vegetative condition of the syntypes.

Polysyncraton pedunculatum is a sympatric species with a similar stalked colony. It is distinguished by its soft, aspicular test, atrial tongue and loose coils of the vas deferens.

Leptoclinides imperfectus (Kott, 1962)
(Figs 28, 159A; Pl. 3E)

Askonides imperfectus Kott, 1962: 294 (part, holotype, from Reevesby I.).
Leptoclinides imperfectus: Kott, 1998: 86.
Leptoclinides rufus: Kott, 1972a: 16 (part, specimen from Port Noarlunga); 1975: 9 (part, specimens from 25m).

NEW RECORDS. Western Australia (Albany, QM G302883). Great Australian Bight, off Ceduna, SAM E2507; 32°24'S 133°30'E, QM G9281). Tasmania (Waterford Bay SAM E2842).

PREVIOUSLY RECORDED. South Australia (Elliston Reef – QM G9283, SAM *E2509* Kott, 1975; Reevesby I. – AM Y1348 holotype Kott, 1962; Port Noarlunga – SAM E2604 Kott, 1972a).

COLONY. Colonies are thick, irregular masses or investing sheets, around weed stalks or on flat substrates, 0.5–1cm thick, with dome-like to conical protuberances up to 1cm in diameter, each with a central, apical, cloacal aperture. These protuberances sometimes are separated from one another only by a narrow crease, but in other less regular colonies the occurrence of these swellings is more random. Between the branchial apertures, the surface of the colony sometimes has pointed spicule-filled papillae which occasionally also are present inside the cloacal apertures in the roof of the cloacal cavities. The cloacal apertures open from large chambers in the centre of each surface swelling, and atrial apertures open directly into the roof of the cavities as well as into the oesophageal canals that extend between clumps of zooids around the periphery of the central chambers. Most of the zooids are in the roof of the primary cloacal cavities and have their whole abdomen bent up against the thorax.

An opaque, layer of crowded spicules is at the surface. A conspicuous spicule-free superficial layer of bladder cells is not present. The spicules become less crowded toward the lower half of the colony. In one colony (QM 302883) they form a layer in the floor of the cloacal cavity and are less crowded but usually present at abdominal level and on the base. Three vertical spicule-filled ridges in the branchial siphon lining are seen from the surface as arcs or small clumps of spicules sometimes outlining one or more lobes of the stellate aperture. A clear spicule-free area of test over the anterior end of each zooid surrounds each branchial aperture or sometimes small spicules are present around each aperture, gradually merging with the surface spicules between the apertures.

Spicules are of moderate size, generally not more than 0.04mm in diameter, but occasionally larger spicules, up to 0.1mm are found. Eleven to 13 conical rays are in optical transverse section but are of two types, one with chisel-shaped tips and the other with short truncated, flattened tips

A colony from Elliston Reef (QM G9283) is reported to have been 'mostly grey with orange around the siphons' (probably the cloacal apertures) and 'reddish-brown' in life. The colony from Port Noarlunga (SAM E2604) was orange to light fawn in life and the one from Albany (QM G302883) had a grey, orange and red marbled pattern.

A cloacal cavity was not detected in the hard, thin, and smooth colonies (QM G9281, QM G302883) with juvenile thoraces that do not open to the surface.

ZOOIDS. Zooids are just under 2mm long overall, although usually less owing to contraction of the thorax. Thoraces are wide, with about 10

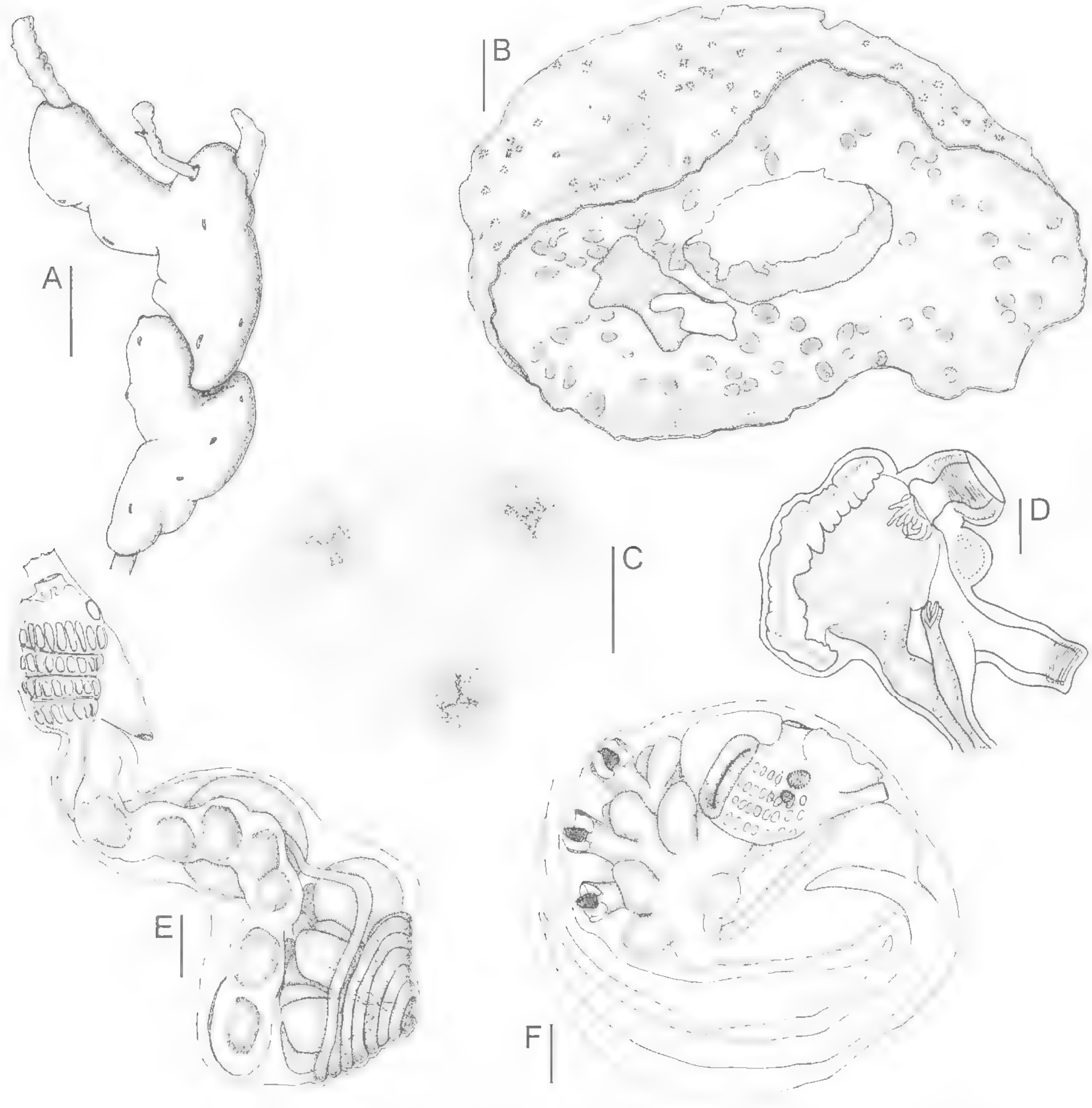


FIG. 28. *Leptoclinides imperfectus* (A–C,E, QM G9283; D, SAM E2842; F, AM Y1348) – A, colony from upper surface; B, semidiagrammatic vertical section through a colony showing spicule distribution (the central cavity accommodates the weed stalk around which it has grown); C, branchial apertures; D, thorax; E, zooid, the thorax probably a juvenile vegetative one; F, larva. Scales: A, 1.0cm; B, 1.0mm; C, 2.0mm; D, 0.5mm; E–F, 0.1mm.

fusiform stigmata per row, and posteriorly oriented atrial siphons extending from their postero-dorsal corners. The branchial siphons are long and cylindrical and the aperture is not lobed. A flat, circular lateral organ to 0.09mm diameter is on each side of the thorax opposite the last row of stigmata. Fine thoracic longitudinal muscles are conspicuous on the anterior body wall. Zooids have a particularly long oesophageal neck (half the total length of the thorax). The gut loop is long and rather narrow, with an almost elliptical stomach, a long duodenum with a slightly bulbous distal end, and a small almost spherical posterior stomach. The proximal end of the rectum has a distinct elbow. Sometimes a fecund copepod is in the lumen of the gut. The testis, opposite the relatively short post-pyloric part of the gut loop, consists of 6 to 8 long club-shaped follicles, arranged in a circle. The vas deferens coils 7 times.

Eggs are present in some specimens either anterior or posterior to the zooids (possibly moving back following fertilisation). The specimen from the Great Australian Bight with juvenile thoraces (QM G9281) has maturing testes but no eggs. It may be protandrous, the eggs developing after the thoraces have completed their regeneration and the cloacal cavity has reappeared. Tailed larvae are found in the type specimen collected in December. The larval trunk is about 0.6mm long. The tail is wound almost the whole way around it, and there are 4 lateral ampullae on each side of the 3 median adhesive organs.

REMARKS. The stellate spicules with chisel-shaped rays resemble those in *L. maculatus* and some with truncated rays are also present in the latter species. The species are distinguished by the colony form, pigment distribution and absence of a spicule free superficial layer of bladder cells in the present species.

The colony resembles *L. dubius* with dome-like swellings and spicules in the surface layer of test. However, it has none of the characteristics of the *dubius* group. Tropical *L. cavernosus*, which Kott (1962) originally thought was conspecific with the present species, has spicules of similar form and distribution, and similar numbers of testis follicles. However, it has larger zooids, a superficial layer (albeit thin) of bladder cells, a different larva and spicules with more numerous and more sharply pointed rays.

In the temperate *L. compactus* a conspicuous superficial bladder cell layer lacks spicules, while in the present species the superficial layer of test is packed with spicules and there is no obvious bladder cell layer. *L. coelenteratus*, another species with large uninterrupted cloacal cavities, has larger zooids and spicules with more and shorter (and sometimes quite blunt) rays.

Leptoclinides kingi Michaelsen, 1930
(Figs 29, 161D; Pl. 3F)

Polysyncraton dubium: Hartmeyer, 1919: 136.
Leptoclinides dubius: Michaelsen, 1930: 507 (*f. kingi*). Kott, 1962: 289 (*f. kingi*).

NEW RECORDS. Western Australia (Buccaneer Archipelago QM G302870). Queensland (Wistari Reef, QM GH234; Whitsunday I., QM GH5369; Haslewood I., QM GH 5373).

PREVIOUSLY RECORDED. Western Australia (Cape Jaubert – Hartmeyer 1919; Shark Bay – Michaelsen 1930). Queensland (Hervey Bay – QM G9284 Kott, 1962; Campwin Reef, Sarina – QM G4962 Kott, 1962).

COLONY. Colonies are large, fleshy sheets, with the surface raised into rounded ridges and other (sometimes irregular) prominences. Common cloacal apertures are apical or evenly spaced along surface ridges. Sometimes narrow branches of the colony subdivide and anastomose to form a fleshy 3-dimensional reticulum. Spicules are crowded in the surface test, and also in the minute papillae that sometimes project from the surface between the branchial apertures. Spicules also are in a layer in the base of the colony. Elsewhere in these fleshy colonies the spicules are either absent or scattered sparsely. Spicules in the superficial layer are sometimes separated into clumps rather than being evenly spaced. Some of the ridges and irregularities on the surface appear to result from thickened test rather than the size of the cloacal cavities, although the large cavities beneath the cloacal apertures cause many of the surface elevations. Sometimes a branch of the colony has a large central common cloacal chamber, interrupted only by occasional test connectives from the surface zooid bearing layer to the basal test. Common cloacal canals penetrate the test posterior to the zooids. Atrial apertures sometimes open directly into posterior abdominal cavities and sometimes into narrower secondary canals at oesophageal level.

Spicules are small (to 0.04mm diameter), generally with 13–15 broadly based conical pointed rays, although some are spherical with flat-ended rays. Spicules line the branchial siphons and from above the star-shaped apertures are outlined by a line of white spicules.

Living colonies are reported to have been light yellow, green (QM G302870).

ZOOIDS. Zooids are small and contracted in the examined colonies. The branchial aperture has shallow lobes and is on a short siphon with a branchial velum in the base forming a false siphon. The atrial aperture is on a relatively short, posteriorly oriented siphon, with a smooth rim. The branchial sac has 10–12 round-tipped stigmata per row. The distal part of the gut loop is flexed ventrally up against the pyloric part to form a secondary loop. A spherical mass of 9–16 male follicles has the sperm duct making an S-bend on its outer surface. One small egg is present on the outside of the testis in the examined specimens.

Larvae, present in colonies from Sarina (QM G4962) in August (Kott, 1962) and from Wistari Reef (QM GH234) in November, are large, with a

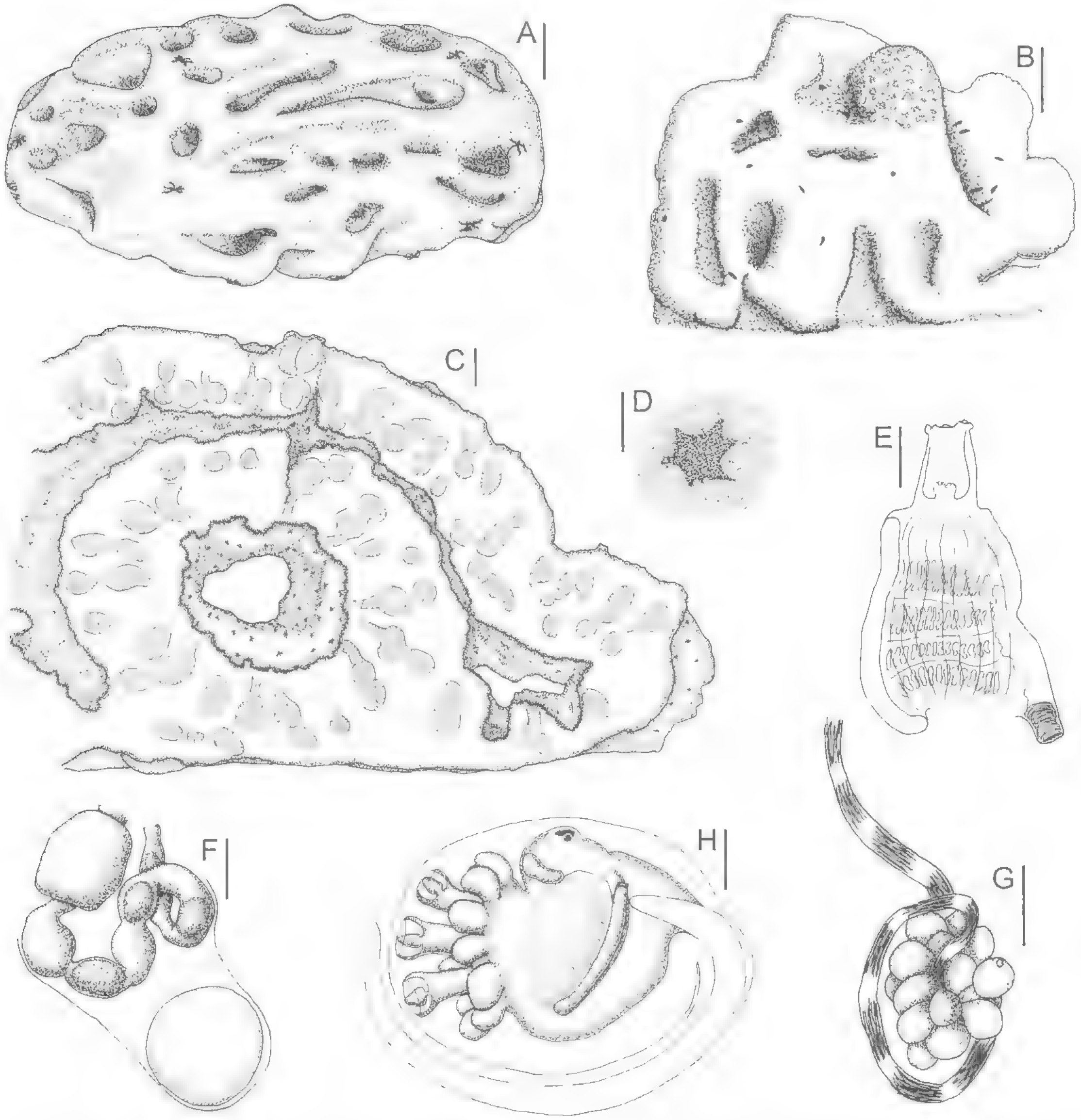


FIG. 29. *Leptoclinides kingi* (A,C, QM G302870; B,D, QM GH234; E–H, QM G4962) – A,B, colonies; C, semidiagrammatic vertical section through colony showing horizontal posterior abdominal cloacal cavity and some branchial apertures opening from a central internal space resulting from folding of the colony; D, branchial aperture from above showing spicules in lining of branchial siphon; E, thorax, showing false siphon in base of branchial siphon; F, abdomen showing double gut loop and large egg; G, grape-like cluster of male follicles and vas deferens; H, larva. Scales: A,B, 1.0cm; C, 1.0mm; D–H, 0.2mm.

trunk 1.2mm long, and 6–8 pairs of lateral ampullae.

REMARKS. The fleshy colonies resemble those of most species of the *dubius* group in having a single layer of spicules in the superficial test and spicules outlining the margins of the stellate branchial apertures. The zooids also are similar, having a branchial velum forming a false siphon, a double gut loop, and a large spherical testis with many follicles and an S-shaped course of the vas deferens on the surface of the testis.

Zooids of the present species may be smaller than *L. dubius*, but this could be only apparent, resulting from contraction. Kott (1962)

distinguished *L. dubius* f. *kingi* from *L. dubius* f. *typicus* by its better developed cloacal chambers. However this probably is associated with colony size, and a more reliable character distinguishing the species from others in the *dubius* group is the form of the spicules. In the present species spicules are mostly those with conical rays; and the longer slate-pencil-like and fusiform rays common in *L. levitatus*, *L. dubius* and *L. multilobatus* are not found. Spicules resemble those of *L. durus*, although in the latter species they are crowded throughout the test rather than being in a single layer at the surface. The larvae are the same size as the smaller ones of *L. dubius*, with similar lateral ampullae.

Leptoclinides levitatus sp. nov.
(Figs 30, 160-I; Pl. 3G)

TYPE LOCALITY. Queensland (Little Black Reef, 19°46.25' 149°22.0'E NW face, 15m, coll. AIMS Bioactivity Group 21.10.87 Q66C0909, holotype QM GH5380). Western Australia (Warnbro Sound near Rockingham, coll. AIMS Bioactivity Group 20.3.89 Q66C2776, paratype QM GH5456).

FURTHER RECORDS. Queensland (Penrith I., QM G308700).

COLONY. Both type colonies are large, with a thick (to 2cm) layer of basal test separated from the upper zooid layer by extensive cloacal cavities and the surface raised into long rounded ridges. Large circular common cloacal apertures are spaced at random along the highest part of the ridges. They are not conspicuous in the preserved material but they are in life. The colony from Penrith I. is a large irregular mass, with protruding conical lobes with a central mass of test continuous with the basal test. The outer surface is smooth but there is no superficial bladder cell layer. Small spicules are found in crowded clumps or in an even layer in the surface test and lining the common cloacal cavity. They are scattered more sparsely through the remainder of the test. They fill the lining of the branchial siphon, but there is no interruption in their distribution between the branchial lining and the surface layer of test. Thus, although star-shaped apertures are evident they do not appear to be outlined by a single marginal row of spicules. Spicules are up to 0.04mm in diameter with 13 to 15 rays in optical transverse section. The majority have long, pointed rays of different lengths (in the one spicule) but some have fusiform, or blunt and rod-like or slate-pencil-like rays. Some of the smaller spicules are almost

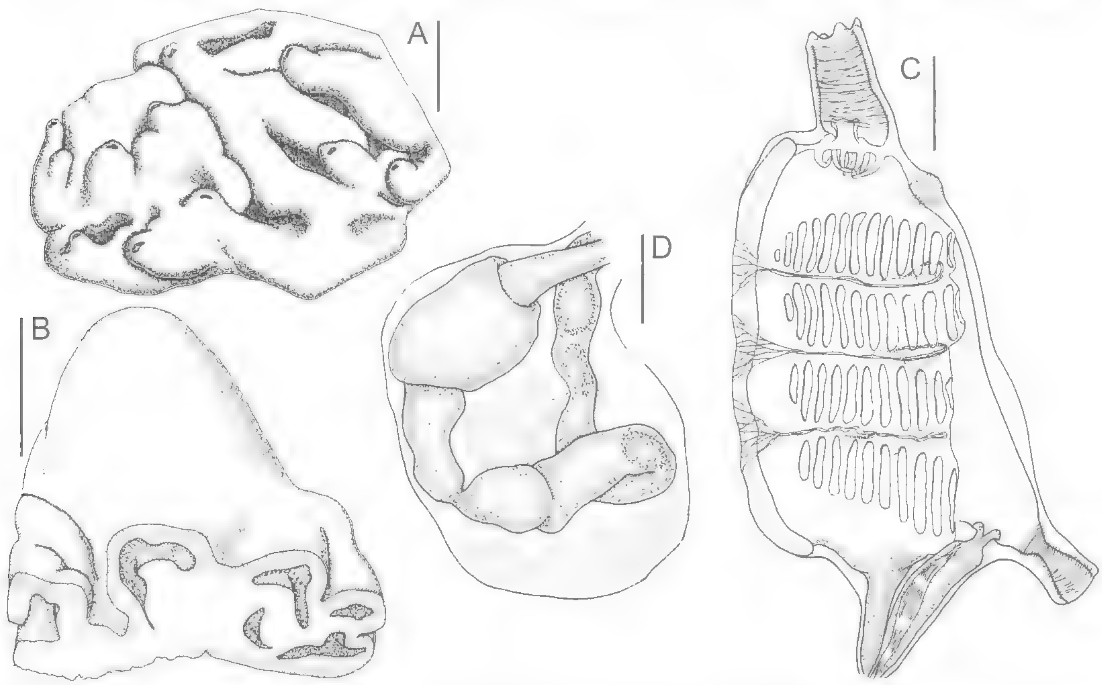


FIG. 30. *Leptoclinides levitatus* sp. nov. (A,D, QM GH5456; B,C, QM GH5380) – A,B, colonies; C, thorax showing false branchial siphon; D, abdomen showing double gut loop. Scales: A,B, 2.0cm; C,D, 0.2mm.

globular with flat-tipped rays and occasionally the rays have chisel-shaped or divided tips.

All specimens were photographed in situ. The holotype was bright orange-red, the paratype pink with patches of green that may have been symbionts (possibly *Prochloron*) on the surface, and the other colony was black. All are white in preservative.

ZOOIDS. The branchial siphon is long, with a short velum forming a short false siphon in its base. The branchial sac has 10 to 14 stigmata per row, the anterior row having 13 on the right and 14 on the left. The gut loop is long, its posterior pyloric part being bent up to form a secondary loop. The numerous (up to 15) male follicles are clumped together to form a spherical three-dimensional mass and the vas deferens forms an S on the outer surface of the spherical mass of male follicles.

REMARKS. The discontinuous records suggest a relatively wide range for *L. levitatus*. The species is a member of the *dubius* group, separated from other members of the group by the long rays of the spicules. The spicules have the fusiform and slate-pencil-urchin type rays found in *L. dubius*, although the shorter-rayed spicules of the latter species do not occur and the spicule rays are less numerous (13 to 15 in optical section). The spicule rays of *L. echinus* are equally long but always pointed and not as variable in length as in *L. levitatus*. The spicules resemble those of *L. durus* but they are not crowded throughout as they are in the latter species and they have longer rays.

Leptoclinides lissus Hastings, 1931
(Fig. 160F)

Leptoclinides lissus Hastings, 1931: 93. Millar, 1963: 704. Kott, 1998: 86.
Not *Leptoclinides lissus*: Brand et al., 1989: 425 (<*L. brandi*).
?*Leptoclinides rufus*: Eldredge, 1967: 220 (part, specimens from Auau Channel, Hawaii, without a bladder cell layer).

PREVIOUSLY RECORDED. Queensland (Low Is – holotype AM G13449). ? Hawaii (Eldredge, 1967).

COLONY. Colonies are flat sheets with a relatively smooth upper surface without a superficial bladder cell layer. Branchial openings are marked by a few spicules clustered in the apertures — in the centre of otherwise spicule-free areas over the anterior ends of the zooids. Spicules are moderately crowded throughout. They are stellate, to 0.05mm in diameter with 9–11 conical rays in optical section. Common cloacal canals are posterior abdominal, and found especially around the outside margin of the relatively thin colonies, raising ridges on the surface. Large common cloacal apertures are irregularly placed along these ridges.

ZOOIDS. Zooids are relatively small, about 2mm long. The branchial aperture is 6 lobed. The atrial aperture is posteriorly oriented on a short siphon. Stigmata are in 4 rows with about 14 in the anterior row. The gut forms a relatively simple short loop. Male follicles are in a ring of 4–7, tapering to the vas deferens which is wound 6 times around the outer half of the testis.

REMARKS. The species most closely resembles *L. placidus* from the central eastern coast. It is distinguished by its even, upper surface without a superficial layer of bladder cells, absence of spicules over the anterior end of zooids, and regularly stellate but relatively small spicules with pointed rays. Larvae are not known. It lacks the recurved gut, false siphon, marginal spicules lining the branchial apertures, the diversity of spicules and 3-dimensional testis of the *dubius* group. The testis, gut and spicule shape are similar to those of *L. brandi*. However, spicules and zooids are smaller and the spicules are crowded throughout. *L. brandi* has other characteristics of zooid and colony that distinguish it from the present species.

Leptoclinides longicollis sp. nov.
(Figs 31, 159D)

TYPE LOCALITY. Queensland (Moreton Bay, coll. W. Stablum 6.10.80, holotype QM G300898).

COLONY. The colony consists of a number of lobes, each with a terminal common cloacal aperture. Each lobe is about 1cm high and about 1cm in diameter. Extensive posterior abdominal cloacal cavities surround the solid central core of test separating it from the surface zooid-bearing layer. A superficial layer of bladder cells is thin. Also bladder cells are conspicuous, in the central test core. Some black pigment persists amongst the bladder cells in the superficial layer, and in the test lining the common cloacal cavities. Spicules are in a continuous layer or in patches beneath the superficial layer of bladder cells; and they project up into it around each branchial aperture. A few spicules are in the branchial siphonal linings and appear (from the surface) to be clumped together in the centre of the aperture. Spicules are absent from the central test core. Most have 9–11 pointed conical rays in optical transverse section, and are about 0.05–0.06mm in

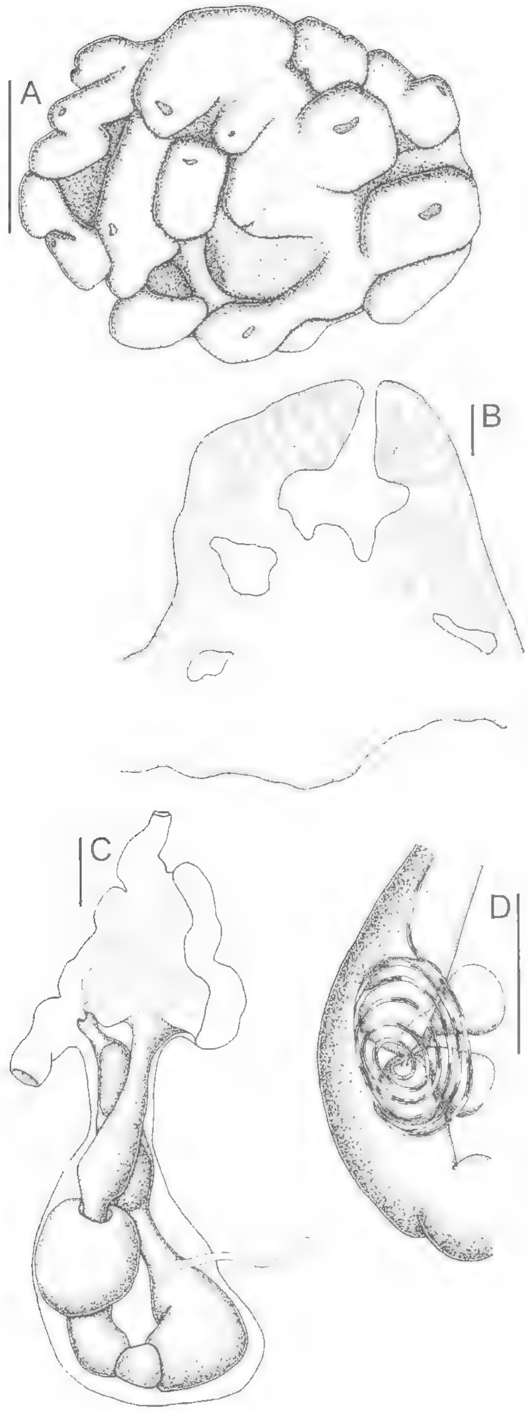


FIG. 31. *Leptoclinides longicollis* sp. nov. (QM G300898) – A, colony; B, semidiagrammatic vertical section through colony lobe showing common cloacal cavity and the position of zooids; C, zooid; D, testis with vas deferens. Scales: A, 2.0cm; B, 2.0mm; C,D, 0.2mm.

diameter. A few smaller spicules have more numerous and finer rays.

Some juvenile zooids are in the base of the central test core, together with the terminal ampullae of long, delicate vascular stolons. The thorax and abdomen of the juvenile zooids appear to be 'same-age' replicates.

ZOOIDS. Zooids are about 2.5mm long, from the smooth-rimmed aperture at the anterior tip of the rather long branchial siphon to the posterior tip of the abdomen. The branchial siphon is relatively long and narrow in the type. The thorax (including the branchial siphon) and the abdomen are of about equal length. The atrial siphon projects posteriorly from the postero-dorsal corner of the thorax. A circular lateral organ depressed into the parietal wall of the thorax is about 0.1mm diameter. The oesophageal neck of the zooid is relatively long, being about half the length of the whole abdomen. The number of stigmata could not be counted in adult zooids, although there are 11 per row in juvenile zooids. The gut forms a vertical loop, or is bent ventrally at right angles to the long axis of the thorax. The almost spherical stomach, the relatively long and distally expanded duodenum, and the oval posterior stomach in the pole of the loop are similar to other species of the genus. The rectum is especially wide at its proximal end. Behind the gut loop are 4 or 5 male follicles converging to the vas deferens, which is wound 5 times around the outer half of the testis.

One to 3 delicate and relatively long vascular stolons arise from the ventral abdominal body wall in the gut loop at the level of the posterior end of the stomach. These vascular appendages sometimes extend into the central test core.

REMARKS. The species resembles *L. rufus* in its firm, gelatinous basal test containing bladder cells, and in the form of the testis and number of vas deferens coils. However, it differs in the form of the colony, *L. rufus* having a more or less flat, even surface, while the present species has lobes with central test core and terminal common cloacal apertures. Further, the long oesophageal neck and the relatively thin superficial layer of bladder cells distinguish the present species. The high lobes of the present colonies, supported by the central test core (which is separated from the outer zooid-bearing layer by an extensive system of posterior abdominal cloacal canals) distinguishes it from species in the *coelenteratus* group (which has raised surface mounds or lobes that are formed by large cloacal cavities beneath

the apertures. Other species with a central test core supporting vertical lobes of the colony are *L. fungiformis* (which is distinguished by its stalk) and *L. compactus* (which has smaller zooids and a more irregular colony).

The presence of juvenile zooids in the basal test is of particular interest. These replicates are not the usual ones produced by oesophageal budding, in which the replicated thorax is joined with the parental abdomen and the reverse. They have, instead, both thorax and abdomen apparently of the same age and status. These clones occurring in the same part of the test as the terminal ampullae of test vessels, may indicate that another method of budding occurs (see discussion on replication in the Didemnidae, above).

Leptoclinides maculatus sp. nov. (Figs 32, 159G; Pl. 3H)

Leptoclinides rufus: Kott, 1972a: 16 (part, specimens from Port Noarlunga and Wright I.)

TYPE LOCALITY. South Australia (Yorke Peninsula, Point Turton jetty piles, 3-4m, coll. K.L. Gowlett Holmes 31.12.93, holotype SAM E2609; Port Noarlunga, on *Ascidia sydneiensis*, 8m, coll. H. Duyverman 10.11.76, paratype QM G9303; Tipara Reef, coll. S. Shepherd 13.5.82, paratype QM G301572).

FURTHER RECORDS. South Australia (Point Turton jetty, SAM E2617, E2618, E2645, QM G302877; Rapid Head, SAM E2659; St Vincent Gulf, SAM E2673 Kott, 1972a; Investigator Strait, QM G302768). Victoria (Western Port, QM G308488, G308556, G308563-4).

COLONY. Colonies are extensive, thin sheets about 3mm thick, with a smooth and even upper surface and sessile cloacal apertures. Dark pigment is in fine, irregular, and branched particles sometimes in, but especially crowded beneath, a thin superficial layer of bladder cells. Pigment particles also are scattered amongst the spicules, becoming sparser toward the middle of the colony, but are not in the basal, spicule-free layer of test. Sometimes the pigment is gathered into evenly distributed small black spots, about 3mm apart, or larger irregular patches, in the superficial spicule-free bladder cell layer of test. Common cloacal apertures are inconspicuous and scattered over the surface. The cloacal cavities are deep vertical spaces surrounding clumps of zooids. These expand into posterior abdominal spaces and spaces that penetrate the zooid clumps at oesophageal level. The surface of the colony is depressed over the deep primary common cloacal canals.

Moderate sized spicules to 0.07mm diameter, with 9–11 usually conical rays, with chisel-shaped and occasionally truncated tips sometimes are in the superficial layer of test, but mostly are crowded in a layer beneath it, becoming less crowded around zooids. They occur in the floor of the cloacal cavities, but usually are sparse or absent in the basal half of the colony. Three small groups of spicules are clumped or in radial lines in the branchial apertures.

The colony is quite tough but rather pliable, like leather. Colonies from Port Noarlunga are white with grey or dark zooids (Kott, 1972a) but this may result from a misinterpretation of the dark pigment spots. Identical preserved colonies from Wright I. were reported as uniform bluish or light grey and mottled white. Photographed specimens often are white with evenly distributed spots or patches of pigment.

ZOOIDS. Zooids are relatively small, the thorax and abdomen each less than 1.0mm long, although the thorax especially is contracted in the examined specimens. The branchial aperture lacks lobes. The atrial aperture is on a laterally or posteriorly directed siphon from about half way down the thorax. Eight distinct branchial tentacles of 2 sizes are at the base of the branchial siphon. The branchial sac is wide with about 12 short oval stigmata in the anterior row.

The gut loop is relatively narrow, vertical and teardrop-shaped with a relatively long, narrow stomach, long duodenum, and short rounded posterior stomach. Most zooids in the holotype have a large egg anterior to the testis, which is at the left side of the pole of the gut loop. The testis consists of 4 or 5 long male follicles, with 8 coils of the vas deferens. Larvae are present in the basal test of specimens from St Vincent Gulf in November (QM G9303, SAM E2673) . They have a larval trunk about 0.56mm long with a long tail wound three quarters of the way around it. Three short, thick ectodermal ampullae are along each side of the 3 antero-median adhesive organs, and an unpaired ampulla is in the median line. A large horizontal ampulla projects forward from the left side of the oesophageal region of the larval ectoderm.

REMARKS. The species is distinguished by its regularly spaced pigment spots amongst the bladder cells in the superficial layer of surface test, and its small zooids with their simple vertical gut loop. Its spicules and colonies are similar to those of *L. compactus* and *L. variegatus*, although the spicules are not as large

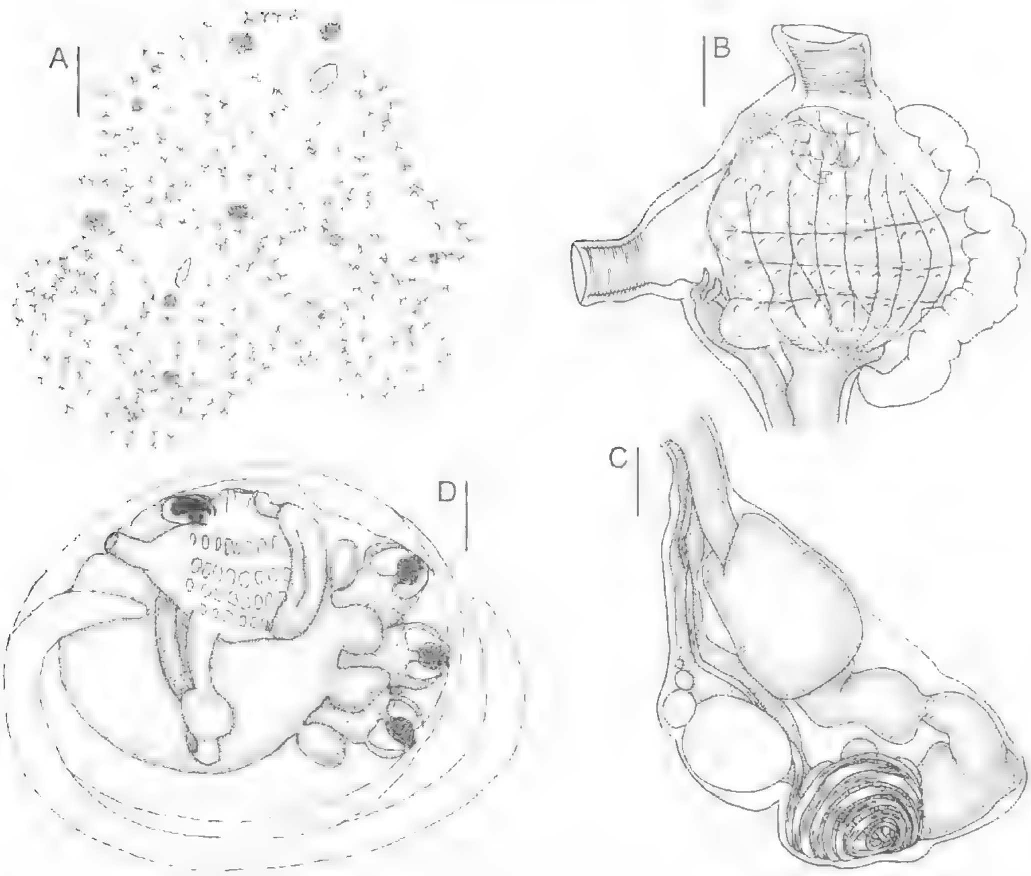


FIG. 32. *Leptoclinides maculatus* sp. nov. (A, QM G301572; B,D, QM G9303; C, SAM E2673) – A, colony surface showing common cloacal apertures (2), position of branchial apertures with triradial rows of spicules and black dots in the surface test; B, thorax; C, abdomen; D, larva. Scales: A, 2mm; B–D, 0.1mm.

as some in the latter species which has its common cloacal apertures confined to the colony margins rather than scattered randomly over the upper surface, as in the present species. *L. aciculus* also has similar colonies and similar but larger spicules and more coils (7) of the vas deferens. The chisel-shaped and truncated spicules are like *L. imperfectus*, although in *L. maculatus* they are smaller with fewer rays. The elevations on the surface of *L. imperfectus* distinguish it from the sheet-like colony of the present species. *L. exiguus* has similar colonies, but spicules lack truncated rays, the common cloacal cavity is more restricted, larvae are smaller and the vas deferens coils only 5 times.

Leptoclinides magnistellus sp. nov.
(Fig. 158F)

Polysyncraton mortenseni: Kott, 1962: 296 (part, specimen from Oyster Bay, Tasmania only).

TYPE LOCALITY. Tasmania (Oyster Bay, 10m, coll. F.I.S. Endeavour 1910-1914?, holotype AM Y1481).

COLONY. The colony, growing over a bryozoan, is hard and brittle with a smooth but uneven surface. Some ridges and irregular to circular swellings and large, open common cloacal apertures are on the highest points of the surface prominences. The surface is raspy to the touch, owing to the large spicules crowded throughout. Branchial apertures are obscured by spicules which plug the siphons. Spicules are stellate, to 0.24mm diameter with 11–13 relatively long pointed conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.35.

The common cloacal cavity is an extensive posterior abdominal space crossed by narrow connectives between the thick, upper zooid-bearing layer of test and the thin basal layer.

ZOOIDS. Zooids are of moderate size, with small branchial siphons, and posteriorly directed atrial siphons. The testis is divided into 5 follicles and the vas deferens coils 3 times around it.

REMARKS. On the basis of the large stellate spicules, Kott (1962) assigned this colony to the New Zealand species *Polysyncraton mortenseni* Michaelsen, 1924. In doing so, she overlooked the posteriorly oriented atrial siphon, spicule differences (the New Zealand species having rounded, rather than long pointed rays) and their particularly large diameter. The other specimens from Tasmania (*Didemnum mortenseni*: Kott, 1954), which Kott (1962) had proposed as conspecific with the present specimen, do not have such large spicules (see *Trididemnum cristatum* and *Polysyncraton tegetum* Remarks, below). Kott (1962) mistook posterior abdominal spaces for cavities created by fusing of parts of the colony. On re-examination these are seen to be true posterior abdominal cavities.

L. confirmatus from Port Davey also has large stellate spicules, but their maximum diameter is 0.14mm and their rays are relatively short. Tropical *L. caelestis* from Western Australia also has spicules to 0.15mm in diameter, but they are fewer and generally have longer rays.

The large spicules of this species are its outstanding character, such large stellate spicules not having been recorded for any other known didemnid..

Leptoclinides multilobatus Kott, 1954
(Figs 33, 161C)

Leptoclinides multilobata Kott, 1954: 166.
Leptoclinides multilobatus: Kott, 1998: 87.
Leptoclinides kingi: Kott, 1972a: 17.

NEW RECORDS. South Australia (Pearson I., QM GH1317; Flinders I., QMGH1321; St Vincent Gulf, SAM E2603). New South Wales (Nambucca Heads, QM G10013, MV F68822; Solitary I., QM G9624).

PREVIOUSLY RECORDED. South Australia (St Vincent Gulf – SAM E2600 Kott, 1972a). Tasmania (off Maria I, AM Y1492).

COLONY. Colonies are fleshy, upright lobes with terminal cloacal apertures, or more extensive with the surface raised into several upright lobes each about 4cm high with a large permanently open terminal common cloacal aperture. One colony (SAM E2603) is a fleshy vertical plate with zooid openings on all external surfaces and one large common cloacal aperture in the centre of the upper rim. The outer layer of test containing the layer of spicules is only loosely attached owing to the very soft internal test and the large cloacal spaces. The test is thickened at the base of the vertical lobes and projects up into them contributing to their prominence and rigidity. Common cloacal canals penetrate the basal test of the colony posterior to the zooids, and surround the central test core of the vertical lobes, separating it from the zooid layer. Secondary canals extend between the zooids at oesophageal level. Spicules are in the superficial test, sometimes crowded in a white, opaque layer but sometimes more sparse or in discontinuous clouds of spicules. A distinct bladder cell layer is not present. A less crowded layer of spicules is on the base of the colony. In the remainder of the test, spicules are moderately crowded to sparse. Spicules line the branchial siphons, appearing from the surface to form a marginal row around each stellate aperture. Sometimes a clear spicule-free area around the aperture appears from the surface as dots alternating with the rays of the stellate opening; but in other specimens this spicule-free area is not present, and spicules lining the siphons are continuous with those in the surface of the colony. Many spicules are almost globular with flat-ended rays; others are stellate with short conical or long, sometimes fusiform, pointed and slate-pencil rays, up to about 15 in optical transverse section. Spicules are mostly 0.015 –0.02mm in diameter, but a few reach the maximum diameter of 0.0275mm. Only the zooids in the vicinity of the cloacal apertures open directly into the primary cloacal cavity. Mostly they open into the secondary cloacal canals at oesophageal level.

Living colonies are reported to have been 'pinky purple' (QM GH1321) or 'pink with dark red-black zooids' (QM GH1317).

ZOOIDS. Zooids are about 3mm long. The branchial aperture, with 6 short points around its rim, is on a long cylindrical siphon with a narrow velum forming a short false siphon in its base (in front of the long tentacles). The atrial siphon is a smooth-rimmed cylinder directed posteriorly from the postero-dorsal corner of the thorax. The branchial sac has 12 stigmata in the posterior row, and 13–14 in the other 3 rows. The distal part of the gut loop is flexed ventrally forming a secondary loop. The testis has 10–20 follicles crowded into a sphere and converging to the centre. A small egg is on the outer side of the testis. The vas deferens forms an S on the testis, or makes one turn around it. Larvae are not known.

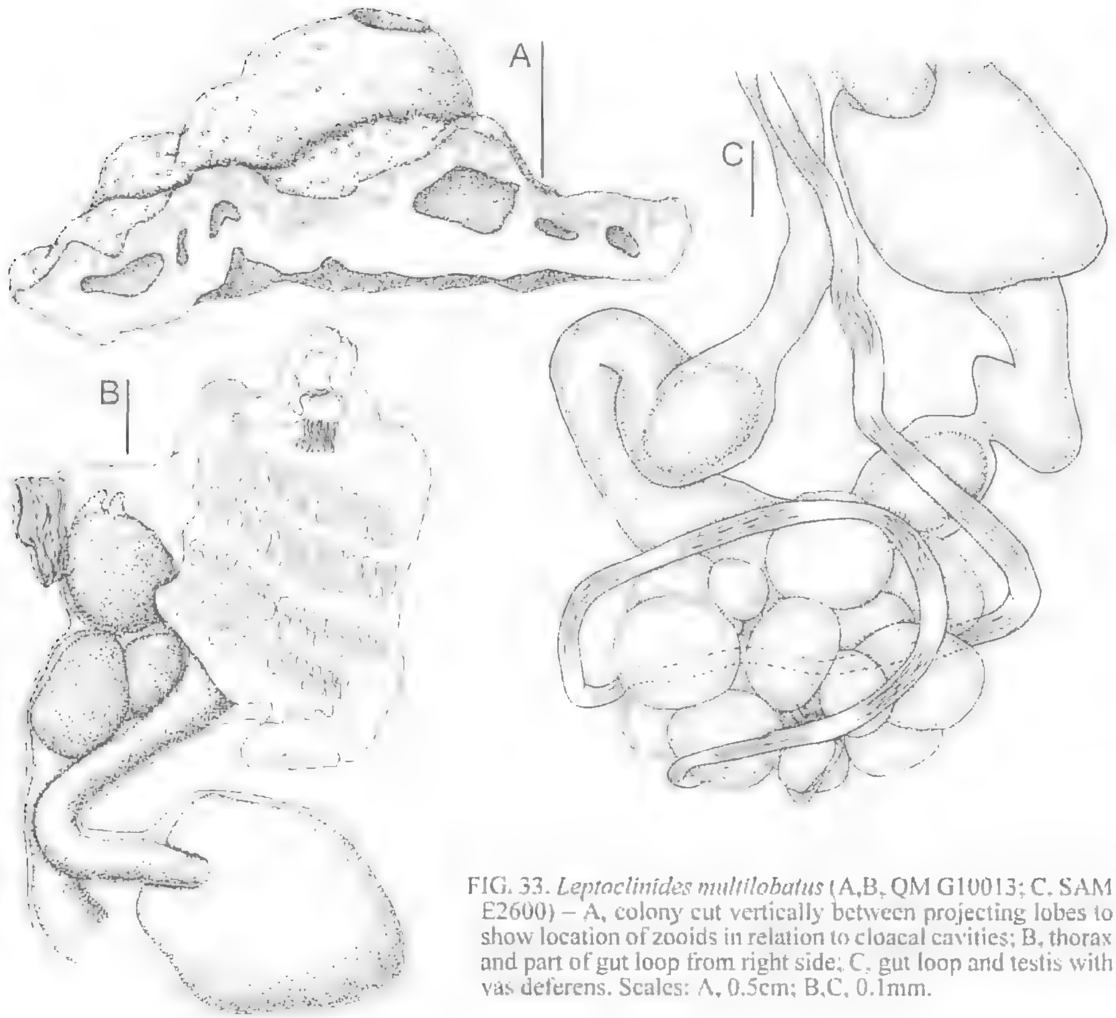


FIG. 33. *Leptoclinides multilobatus* (A,B, QM G10013; C, SAM E2600) – A, colony cut vertically between projecting lobes to show location of zooids in relation to cloacal cavities; B, thorax and part of gut loop from right side; C, gut loop and testis with vas deferens. Scales: A, 0.5cm; B,C, 0.1mm.

REMARKS. Zooids, apart from being smaller, have all the characters of others in the *dubius* group. Although it has the same range of spicule types as *L. dubius*, the present species is distinguished by their smaller size, the smallest known for this genus. *L. durus* has more crowded, larger and less diverse spicules. *L. kingi* also has less diverse spicules; and *L. levitatus* and *L. echinus* have spicules with fewer, longer rays. The present species has distinctive colonies, the surface raised into one or more vertical, flattened to conical protrusions, each with terminal cloacal aperture and central test core with connectives joining it to the outer zooid-bearing layer. Surface prominences in *L. dubius* and *L. kingi* are formed by enlarged cloacal cavities rather than thickened cores of test.

Leptoclinides placidus sp. nov.
(Figs 34, 159-I)

TYPE LOCALITY. Queensland (off Moreton Bay, Smith's Reef, 15m, coll. A. Rozefelds 20.4.81, holotype QM GH372; Moreton Bay, coll. W. Stablum 8.10.80, paratypes QM G300902).

FURTHER RECORDS. New South Wales (Byron Bay, QM G308515; Solitary Is, QM G9623; Nambucca Heads, QM G10027). Queensland (Hervey Bay, QM G9285).

COLONY. Colonies are firm investing sheets with a superficial layer of bladder cells. Some grow over weed, and one extensive colony (QM G300902) surrounds a clump of barnacles. The surface is relatively smooth without marked surface swellings except where the large common cloacal apertures are slightly raised. Cloacal apertures are around the margins of the colony. The common cloaca is an extensive

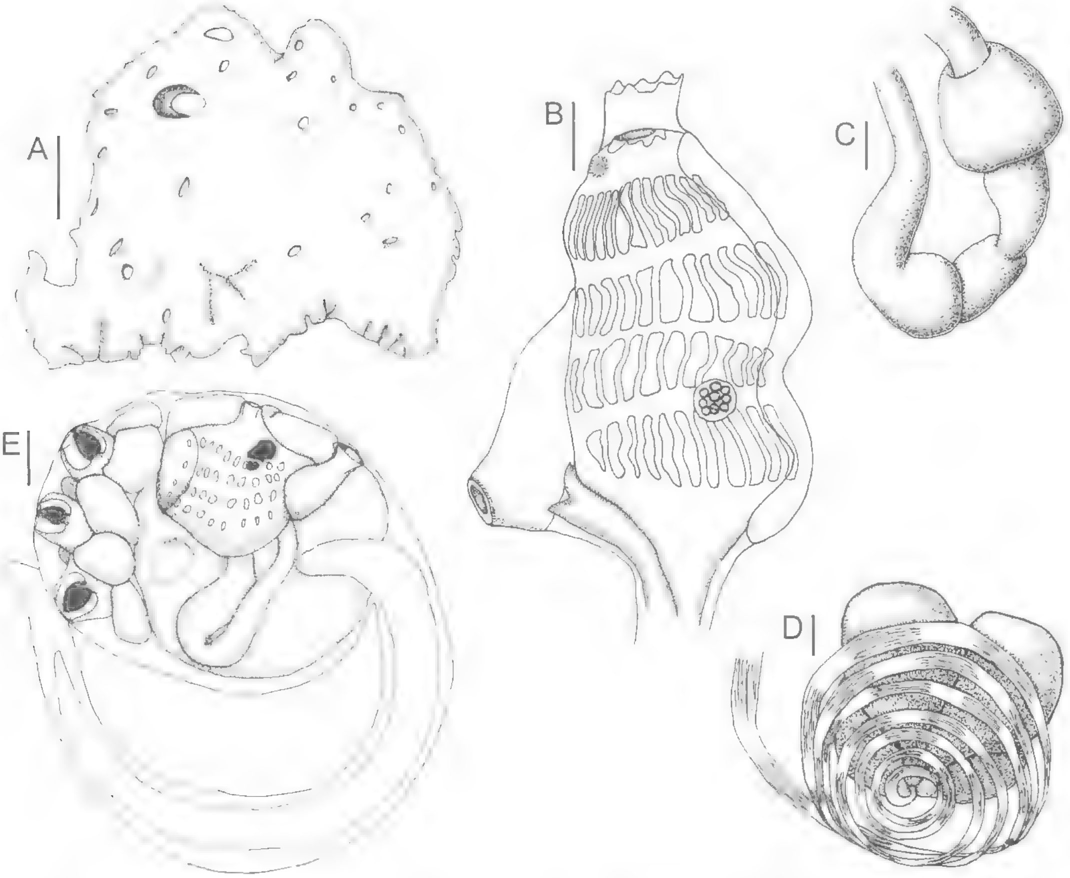


FIG. 34. *Leptoclinides placidus* sp. nov. (A, QM GH372; B-E, QM G9623) – A, colony from above showing raised common cloacal apertures;b, thorax; C, gut loop; D, testis and vas deferens; E, larva. Scales: A, 1.0cm; B–E, 0.1mm.

horizontal space beneath the zooids, but extending up towards the upper surface around clumps of zooids to partially separate them from one another. Strands of test from each clump of zooids cross the common cloacal chamber and connect the basal to the surface zooid-bearing layers. Spicules are throughout the test although they are not especially crowded anywhere. Occasionally they spread into the superficial bladder cell layer. Three small groups of 2 or 3 spicules are in the branchial siphon lining — visible from the surface of the colony in the centre of each branchial aperture. These clusters of spicules are surrounded by spicule-free rings of test over the anterior end of each zooid. Five short rows of spicules are present around each atrial opening into the common cloaca. Relatively uniform spicules, generally to 0.05mm in diameter but occasionally to 0.08mm have about 9–11 conical rays in optical transverse section with chisel-shaped tips.

The holotype colony is reported to have been orange with grey patches and streaks. In preservative it retains streaks of yellow pigment. Other colonies are white or grey in preservative, but their colour in life is not known.

ZOOIDS. Fully relaxed zooids are up to 2mm long, thorax and abdomen of equal length. Branchial and atrial apertures are on short siphons, the atrial siphon posteriorly directed. A large (to 0.1mm diameter) circular lateral organ is on each side of the thorax, opposite the interspace between the middle of the third and fourth rows of long, narrow stigmata. About 14 stigmata are in the anterior row of the branchial sac. The gut forms a simple vertical loop, and is divided into stomach, duodenum with a slight expansion at its distal end, oval posterior stomach in the pole of the loop, and a rectum with its widest diameter

proximally. Testis of 3 or 4 follicles tapering to the vas deferens which winds 7 times around its outer half.

Embryos are in the basal test of the colonies from Moreton Bay in April and from the Solitary Is. Larvae have a trunk about 0.6mm long, 3 large almost sessile adhesive organs in the anterior mid-line, a median dorsal and a median ventral ampulla and 2 pairs of lateral ampullae. In advanced larvae the adhesive organs and ampullae are on a frontal lobe that is separated from the main part of the larval trunk by a constriction particularly deep ventrally and dorsally.

REMARKS. This species is distinguished from *L. cavernosus* (which also has spicules through most of the test, and a thin superficial bladder cell layer into which the spicules sometimes spread) by its flat colonies lacking surface swellings over the large cloacal cavities, spicules with fewer rays and lacking flat- or round-tipped rays, and fewer testis follicles. Living specimens appear to lack the dark pigmentation sometimes found in the surface test of *L. cavernosus*. *L. lissus* has spicules in the basal as well as upper half of the colony, but they are smaller than in the present species and in *L. lissus* a superficial bladder cell layer is not present. The spicules have fewer rays, the superficial bladder cell layer is thinner than in *L. rufus* and spicules are present throughout the test (rather than in a single layer beneath the bladder cells). The species also resembles *L. variegatus* from South Australia in the form and pigmentation of the colony but is distinguished from it by more coils of the vas deferens and spicules with fewer rays evenly distributed through all levels of the colony.

Leptoclinides rigidus sp. nov.
(Figs 35, 160C; Pl. 4A)

? *Leptoclinides reticulatus*: Monniot & Monniot, 1996: 178.

TYPE LOCALITY. Queensland (Whitsunday Group: Deloraine I., 10m, coll. AIMS Bioactivity Group 13.10.87, holotype QM GH5371; 7m AIMS Bioactivity Group 3.10.87, paratype QM G300987).

FURTHER RECORDS. Western Australia (Monte Bello Is, QM GH5407). Queensland (Central Great Barrier Reef, QM G302887; Hawksbury I., QM G300954). Northern Territory (Wessel I., QM G302926).? Papua New Guinea (Duke of York Is – Monniot & Monniot, 1996).

COLONY. Colonies are extensive, tough and firm gelatinous sheets about 5mm thick. Zooids are along each side of the deep primary cloacal canals but also form clumps surrounded by these canals and the posterior abdominal spaces. A moderately thick superficial bladder cell layer is present over the upper surface, although some spicules are present amongst the bladder cells. A layer of relatively crowded spicules surrounds the thoraces and projects up through the bladder cells around the branchial siphon of each zooid. The spicules become sparser beneath the thorax layer, and are only very sparse at abdominal and posterior abdominal level. Some spherical clumps of spicules occur in the basal test and in linings of the common cloacal cavities and canals including the posterior abdominal cavities. The base of the colony contains crowded bladder cells.

Spicules are regularly stellate, with 9–11 conical rays, with pointed or chisel-shaped tips, in optical transverse section. Generally the spicules are to 0.07mm diameter, but a few are up to 0.09mm. Ray length/spicule diameter ratio is 0.32.

Colonies are reported to have been mottled grey and white (QM G300954), or beige (QM GH5371) or glistening white (QM G302887). However, the photo of the first of these is black with light rings around the apertures, resembling *L. reticulatus*: Monniot & Monniot, 1996; and the photo of the holotype appears to be more black than beige. Another specimen from the type locality (QM G300987) is said to have been black and green although the photograph shows it to have been black with orange spots. In preservative colonies are cream or white.

ZOOIDS. Zooids are of moderate size, barely 1.0mm long, although the abdomen (from the base of the oesophagus) tends to be bent ventrally (almost at right angles to the longitudinal axis of the body). Often the branchial and atrial siphons are in a line that stretches between the upper surface of the colony and the posterior abdominal cloacal space, so that the thorax lies obliquely to the upper surface, and the distal part of the gut loop is flexed ventrally toward the surface. Both branchial and atrial siphons are long, usually cylindrical, tubes. The rims of both atrial and branchial apertures lack lobes. Round-tipped columnar ectodermal cells project from the body walls. The branchial sac has respectively 15, 14, 12, 11 oval stigmata in the 4 rows. A circular lateral organ (to 0.1mm diameter) with up to 10 spicules is halfway across the thorax opposite the third and fourth rows of stigmata on each side.

The stomach is pear-shaped tapering to the duodenum. A mass of what appear to be tubules of the gastrointestinal gland is in the abdomen.

The gut forms a simple, gently flexed loop with the testis against its dorsal side. The testis consists of up to 8 male follicles arranged in one plane (2 or 3 in the centre, surrounded by a ring of follicles). They taper to the vas deferens on the outer surface of the zooid (postero-dorsally). The vas deferens makes 5 spirals around the testis. Larvae are not known.

REMARKS. Like *L. rufus*, the species has a conspicuous superficial layer of bladder cells and the lower half of the colony is largely without spicules. Unlike *L. rufus* however, the layer of spicules beneath the bladder cell layer occupies half of the colony rather than being a single layer, the bladder cell layer is not as thick as in *L. rufus*, the giant spicules of the latter species are not present, and the number of vas deferens coils is fewer. *L. cavernosus* has spicules in the bladder cell layer, but it has fewer testis follicles and more coils of the vas deferens. The temperate species *L. imperfectus* has up to 8 male follicles crowded in a circle, but 7 coils of the vas deferens, and the spicules crowd out the bladder cell layer completely. *L. albamaculatus* has similar spicules and bladder cell layer to the present species, and the spicules come to the surface over the branchial apertures in the same way. However, spicules are present throughout the test — they are not absent from the lower half of the colony as in the present species. Black pigment cells in the bladder cell layer in preserved specimens are a distinctive feature of *L. albamaculatus* but not of the present species. *L. compactus* and *L. seminudus* have similar but smaller spicules. *L. exiguus* is distinguished from *L. rigidus* by its more restricted circular common cloacal canals with grey pigment over them forming a surface meshwork and a smaller branchial sac (with up to 10 stigmata per row). *L. constellatus* from Hazelwood I. (QM G302924) has a similar colony and similar spicules. It differs only in having 6 (rather than 5) coils of the vas deferens, and fewer stigmata and the present species has some larger spicules.

L. reticulatus: Monniot & Monniot, 1996 is said to have similar characters to the type specimens of *D. reticulatum* Sluiter, 1909. *However, the type specimen of D. reticulatum* is a *Didemnum*, a junior synonym of *D. jedanense* Sluiter, 1909. Monniot & Monniot (1996) recite the generic characters in their description of this species, but the characters recorded that could help to determine the identity of the species they had before them are identical with those of the present species, viz. common cloacal canals encircling groups of zooids, 5 coils of the vas deferens, a larval trunk 0.45mm long with 3 adhesive organs, 2 pairs of lateral ectodermal ampullae, a dorsal and a ventral ampulla and similar spicules. The largest of the spicules shown (Monniot & Monniot, 1996: fig 24B) is 0.046mm in diameter and has 9–11 conical rays with pointed to chisel-shaped tips like the present species. A superficial spicule-free layer is also present. The colour of the living colony resembles that of several specimens of the present species (QM G300987, G300954). The species may be a synonym of the present one, although neither circular common cloacal canals nor clumps of zooids referred to by the authors are apparent in the specimens photographed (Monniot & Monniot, 1996: pl. 4 B). The

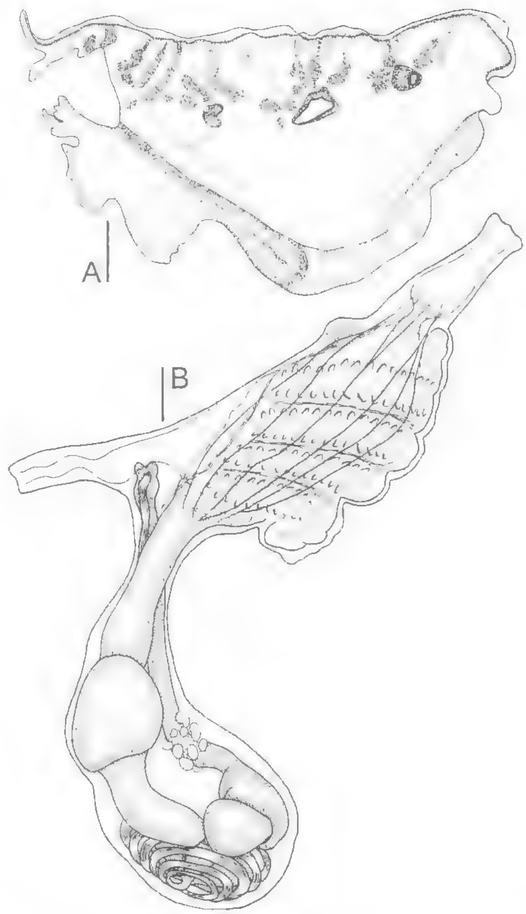


FIG. 35. *Leptoclinides rigidus* sp. nov. (QM G302887) – A, vertical section through colony; B, zooid showing parietal longitudinal muscles. Scales: A, 2.0mm; B, 0.1mm.

spicules and their distribution, and the number of stigmata all resemble *L. sulawesii* Monniot & Monniot, 1996. However, the latter species has different cloacal systems, fewer spicule rays, more coils of the vas deferens (7) than the present one and it becomes red in formalin.

Leptoclinides rufus (Sluiter, 1909)
(Figs 36, 158B; Pl. 4B)

Polysyncraton rufum Sluiter, 1909: 77; 1913: 77.
Leptoclinides rufus: Tokioka, 1952: 92. Kott, 1962: 286 (part); 1998: 87.
Not *Leptoclinides rufus*: Kott, 1971: 37 (?*L. sparsus*); 1972a: 16 (see *L. maculatus*, *L. variegatus*, *L. seminudus*).
Didemnum reticulatum Sluiter, 1909: 60 (part, ZMA TU475.1, TU475.2 and TU475.7 part).
Leptoclinides reticulatus: Hastings, 1931: 92. Kott, 1962: 285. Tokioka, 1967: 89 (part, specimens with single layer of spicules, USNM 11449).
Leptoclinides marmoratus: Millar, 1975: 235.
Leptoclinides oscitans Monniot & Monniot, 1996: 177.

NEW RECORDS. Queensland (Caloundra, QM G308456; Noosa, QM GH1443; G4960-1, G302040; Hervey Bay QM G9458-9, G9463; Bargara QM G9282, G300897; Tannum Sands, QM G4959; Capricorn Group, QM G9461, G10088, GH919, GH1340, GH1361, GH1364, GH5755, G300903-5, G301569, G301571, G301577, G301757, G301772, G301775, G301951, G301975, G302041, G302072, G302083, G302092, G302094, G302122, G302141, G302156, G302184, G302212, G302234, G302395, G302478-80, G302482, G302484, G302528, G302971, G302992; Swain Reefs, QM G308433; Magnetic I., G301722).

PREVIOUSLY RECORDED. Queensland (Low Is – Hastings, 1931). Palau Is (USNM 11449 Tokioka, 1967). Indonesia (ZMA TU840.1, TU840.2 syntypes *Polysyncraton rufum* Sluiter, 1909; ZMA TU475.1, TU475.2, TU475.7, syntypes of *Didemnum reticulatum* Sluiter, 1909; Millar, 1975).

COLONY. Colonies are fleshy with a smooth, shiny, outer surface, often with prominent ridges and depressions and a thick, rounded outer margin. Large common cloacal apertures are randomly scattered along the ridges, or are terminal openings on rounded projections. Most often, the shiny superficial layer of test on the surface of the colony is quite free of spicules. However, some preserved colonies have minute spicule-filled papillae on the surface, spicules continuing up through the bladder cell layer into the papillae from the layer beneath the superficial bladder cell layer. Sometimes spicules also project up into the bladder cell layer around the branchial openings, but in other specimens there is a spicule-free patch over the top of each zooid. The 3 groups or lines of spicules in the branchial siphon lining are visible on the surface of the colony. Spicules are concentrated in the layer beneath the bladder cells and are very sparse in the remainder of the colony, except where an even layer lines the cloacal cavities. The remainder of the test is packed with bladder cells. Large, open, cloacal cavities are beneath the common cloacal apertures. Posterior abdominal canals empty into these cavities from other parts of the colony. Atrial apertures open directly into cloacal cavities, as well as into the canals. Large open cavities in the test are, to some extent, the cause of ridges and prominences on the surface. Sometimes there are 5 lines of spicules where each atrial aperture opens into the cloacal cavity.

Spicules are of moderate size, generally to 0.05mm in diameter, with 13–15 short conical rays in optical transverse section. There also are some sparse, but evenly spaced, giant spicules, to 0.08mm and occasionally to 0.1mm in diameter.

Living colonies have black, and sometimes orange or red irregularly shaped, fusiform, branched or spherical pigment cells in the bladder cell and spicule layers, and orange pigment may be in the body wall of the zooids. The quantity of the different coloured pigments in any part determines the colour of the colony, and in those areas where pigment is absent altogether, the white of the spicules shows through the translucent test so that there is a marble-like pattern. The colours recorded for these colonies are black/orange, red/black, orpiment orange[R]/black, orange/grey, black/tan, slate black[R]/grey/coral red[R] spots, slate grey[R] with maiz[R]e zooids, tan/grey/slate[R], blackish/white/orange streaks, smokey slate[R], brick red[R], burnt umber[R] with olive[R] patches, mottled seal-brown[R]/mouse grey[R], mottled aster purple[R]/black/grey, grey green, purple/green white, grey, and black. Some of the green recorded may be surface symbionts. Some colonies retain a trace of colour in preservative. Most often they are completely white, although some (QM GH1364, G302122, GH1340) retain large ribbon-like dark pigment cells.

ZOOIDS. Zooids range from about 1mm, with a relatively short oesophageal neck, to long zooids with a narrow, vertical gut loop, and a long oesophageal neck. The longer zooids are found around the sides of the cloacal cavities in the most fleshy, well-developed colonies, and the shorter ones are in the zooid-bearing layer of test forming the roof of the large posterior abdominal cloacal cavities. A funnel-shaped to long, narrow branchial siphon has a long sphincter muscle. The rim of the opening is smooth, without lobes. Branchial tentacles are often found directed

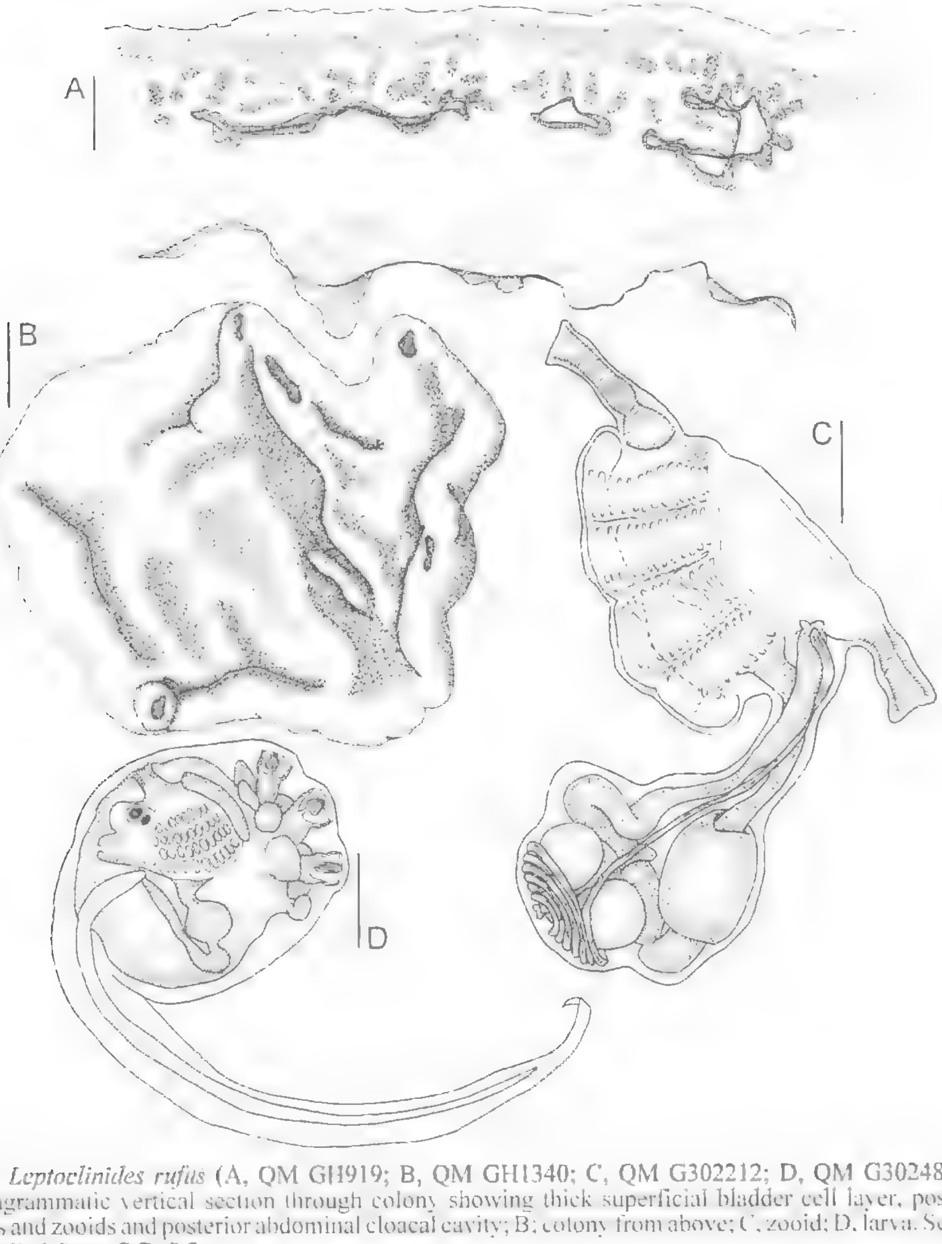


FIG. 36. *Leptoclinides rufus* (A, QM GH919; B, QM GH1340; C, QM G302212; D, QM G302482) – A, semidiagrammatic vertical section through colony showing thick superficial bladder cell layer, position of spicules and zooids and posterior abdominal cloacal cavity; B, colony from above; C, zooid; D, larva. Scales: A, 1.0mm; B, 1.0cm; C,D, 0.2mm.

forwards in a chamber at the base of branchial siphon behind the contracted sphincter muscle. The atrial siphon also has a long sphincter. Sometimes 5 minute papillae have been detected on the rim of the atrial aperture (QM G9461, G301571) but in other zooids these could not be seen. Often they are left in the test when the zooids are removed for dissection. Zooids are not readily removed from these colonies .

A relatively small (about 0.05mm diameter) round lateral organ is between the third and last rows of stigmata on each side of the thorax. Up to 14 long and narrow stigmata were counted in the first row and 12 are in the last row. The duodenum expands distally, the posterior stomach is oval, and a pronounced elbow is at the proximal end of the wide part of the rectum which narrows abruptly about halfway up the ascending limb.

Three to 7 testis follicles are in a single ring, and the vas deferens makes 7 coils around the outer half of the testis. The ovary is at the side of the testis, just anterior to it.

Embryos are being incubated in the basal test in colonies collected at Noosa in May (QM G4960-1), Heron I. in March (QM G302532), August (QM G301577, G302482) and November (QM G302092) and at Magnetic I. in September (QM G301722). The almost spherical larval trunk is 0.7mm long, two broad lateral ampullae are on each side of the adhesive organs and there is a median dorsal and a median ventral ampulla. There is an ocellus and an otolith, the usual 4 well developed rows of stigmata and the tail is wound about two-thirds of the way around the trunk. Occasionally additional smaller lateral ampullae are on one side or other of the trunk.

REMARKS. Distinguishing characters are its thick layer of superficial bladder cells, narrow vertical gut loop with a long oesophageal neck, moderately sized (to 0.05mm) stellate spicules with numerous short conical rays in a single layer beneath the bladder cells with occasional giant spicules about twice the size occurring amongst them, and a large oval lateral organ. The spicules are similar to those of *L. cavernosus* but have fewer rays, and generally are smaller. *L. cavernosus* lacks giant spicules and has spicules throughout the test instead of confined to a layer beneath the bladder cells. Further, *L. cavernosus* has only a very thin layer of bladder cells on the upper surface (most conspicuous around the margin of the colony). The species are readily separated from each other in the field by the thick bladder cell layer and variegated colour pattern of the present species.

The significance of the persistence of pigment cells in preserved colonies of some specimens is not understood. Other characters separating the pigmented from non-pigmented specimens were not detected.

Hastings (1931) and Tokioka (1967) proposed *L. sparsus* Michaelsen, 1924 from New Zealand as a synonym of this species. However, although it has a surface layer of bladder cells, the New Zealand species has smaller spicules and is not conspecific. A tough, irregular, fleshy, specimen from east of New Zealand (USNM12570) wrongly assigned to this species by Kott (1971) has smaller spicules scattered throughout and may be *L. sparsus*.

Millar (1975) proposed *Polysyncraton marmoratum* Sluiter, 1909, *P. ocellatum* Sluiter, 1909, *P. nigropunctatum* Sluiter, 1909, and *Didemnum reticulatum* Sluiter, 1909 as possible synonyms of *L. rufus* (Sluiter, 1909). Of the specimens assigned by Sluiter (1909) to *D. reticulatum*, ZMA TU475.1, TU475.2 and TU475.7 are conspecific with one another and with *L. reticulatus*: Hastings, 1931, and are specimens of *L. rufus*. Other syntypes of *D. reticulatum* Sluiter, 1909, are correctly assigned to *Didemnum* or are *P. marmoratum*. Examination of the types of *L. marmoratus* Sluiter, 1909 and *P. ocellatum* Sluiter, 1909 has shown them to be a single *Leptoclinides* species readily distinguished from the present one (see above, species from adjacent areas). They have a bladder cell layer like the present species but spicules resembling those of *L. dubius*. *Polysyncraton nigropunctatum* Sluiter, 1909 has been confirmed as belonging to *Polysyncraton*. *L. lissus* Hastings, 1931 lacks a bladder cell layer, and also is a distinct species.

Tokioka (1967) included colonies with spicules throughout the test, as well as those with the spicules confined to a layer beneath the bladder cells, in *L. reticulatus*. He also thought that spicules were larger in those colonies in which they were sparsely distributed and that spicule size was not, therefore, a species characteristic. There is no similar correlation between size and concentration of spicules in this or any other known taxon; and Tokioka's specimens are not necessarily conspecific with one another, or with any of Sluiter's specimens. A re-examination of *L. reticulatus*: Tokioka, 1967 has shown only the specimen with spicules from the Palau Is (USNM 11449) to be *L. rufus*. The other colonies from the Palau Is (USNM 11382) with dark pigment and spicules in the surface are not the same species — they have larger spicules, and a relatively thin bladder cell layer. Tokioka's aspicular colony from Kiribati (USNM 11492) also is a distinct species, with a large terminal cloacal aperture and a huge central cavity into which the zooids open directly. Tokioka (1967) suggested that *D. albopunctatum* also could be a synonym of *L. reticulatus* (< *L. rufus*). The lectotype and other specimens of *D. albopunctatum* re-examined by Kott (1981) were found to be correctly assigned to *Didemnum*.

Although the thick superficial bladder cell layer has not been reported for *L. oscitans* Monniot & Monniot, 1996, the species has the characteristic (green, blue-black, grey and orange) marbled colour pattern, large spicules (with numerous short conical rays) in a single

layer at branchial siphon level, and zooids firmly fixed in the tough test. Differences invoked to distinguish the species from *L. rufus* appear to be either within the intraspecific range of variation or to be artefacts.

Generally, *L. rufus* is characterised by its thick surface layer of bladder cells, marbled colour pattern (largely black/orange/grey), 4–7 male follicles, 7 coils of the vas deferens, and rare large (giant) spicules (0.08–0.1mm diameter) evenly scattered amongst smaller spicules (to 0.05mm diameter) with short conical points. Problems in the interpretation and definition of the species are due to variations in the arrangement of the male follicles sometimes in a ring, but sometimes clustered into a circle; and there are variations in the extent to which pigment persists in the preserved colonies, and in the shape of the pigment cells. More than a single species may be involved, but with available data, it has not been possible to resolve this problem. Monniot (1989) referred to a type of *L. rufus* (Sluiter, 1909) in the Senckenberg Museum, Frankfurt. However the syntypes of this species are in the Zoological Museum of Amsterdam (Van der Spoel, 1969).

Leptoclinides seminudus sp. nov.
(Figs 37,160B)

Leptoclinides rufus: Kott, 1972a: 16 (part, specimens from Port Gawler)

TYPE LOCALITY. South Australia (St Vincent Gulf off Port Gawler, growing on *Pinna* and *Cellepora* spp., 18-20m, coll. S.A.S. Shepherd 11.2.67, holotype SAM E2671).

FURTHER RECORDS. Victoria (Western Port, QM G302943). Tasmania (King I., QM G302940).

COLONY. Colonies are extensive, thin sheets sometimes (SAM E2671) only about 2mm thick, dirty beige to pinkish beige in preservative. One of the colonies is said to have been black and yellow in life, although in the deck photograph it is black. A superficial layer of bladder cells is spicule-free or contains relatively sparse but evenly distributed spicules. Beneath this is a layer of evenly distributed but not crowded spicules at zooid level in the upper part of the colony, and the basal one-third of the colony is gelatinous, and without either spicules or zooids. Branchial apertures on the surface of the colony are inconspicuous with irregular clumps of spicules in the siphon lining. Spicules are to 0.06mm diameter with 9–11 conical rays in optical transverse section. The ray length/ spicule diameter ratio is about 0.25. The rays are conical and pointed or chisel-shaped. The common cloacal cavities consist of rather limited spaces that penetrate around the zooids at oesophageal level and the deep primary canals which extend the full length of the zooids but are never posterior-abdominal. Thoraces are embedded firmly in the surface test, and abdomina are in the test beneath the common cloacal cavity. Zooids are impossible to remove from the test.

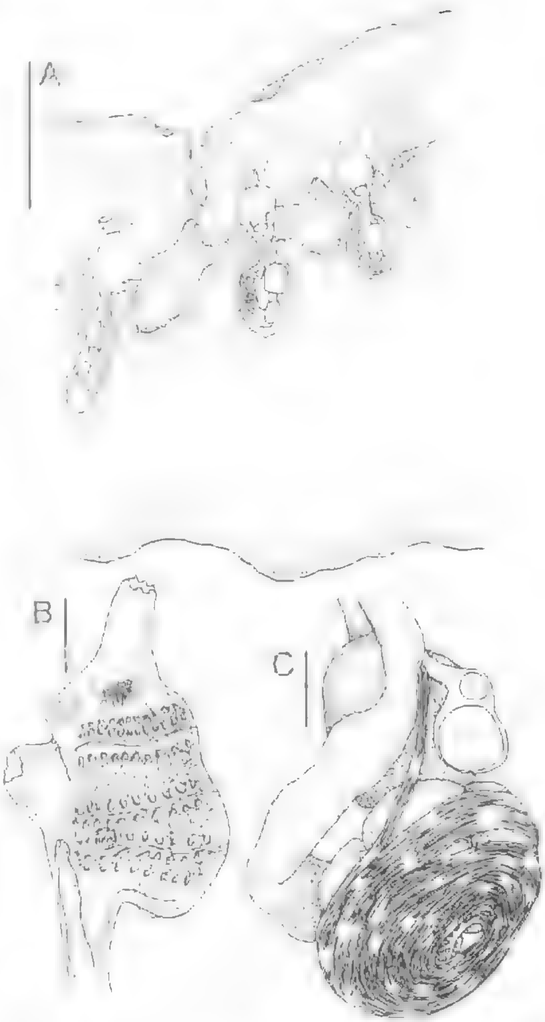


FIG. 37. *Leptoclinides seminudus* sp. nov. (QM G302943) – A, semidiagrammatic vertical section through colony; B, thorax; C, abdomen. Scales: A,1.0mm; B,C, 0.1mm.

ZOOIDS. Zooids are robust (about 1.2mm long), the branchial aperture lacks lobes around its rim and is on a moderately long siphon. The short, muscular atrial siphon projects from the postero-dorsal corner of the thorax. Twelve

stigmata are in the anterior row in the branchial sac, 10 are in each of the next 2 rows, and 8 are in the posterior row. The gut loop is quite open and rounded, and the post-pyloric part is flexed ventrally. A large testis, divided into about 6 or 7 follicles is against the distal part of the gut loop and is surrounded by 8 coils of the vas deferens.

Some embryos are being incubated in the basal test of the holotype. The tail is wound three quarters of the way around the 0.4mm long larval trunk. An otolith, an ocellus, and 3 antero-median adhesive organs are developed, but other larval organs are not.

REMARKS. Colonies are unusually thin for the genus, and the common cloacal apertures are sessile, not raised on surface elevations as in sympatric *L. compactus* and *L. imperfectus*. Further, the relatively restricted, circular common cloacal canals, lined by zooids, that do not penetrate posterior to the zooids are an unusual feature in this genus. The relatively numerous vas deferens coils are also a distinctive character. Other sheet-like *Leptoclinides* species from southern Australia (*L. compactus* and *L. maculatus*) have a superficial bladder cell layer containing some spicules, chisel-shaped as well as pointed spicule rays and spicules sparse or absent in the basal half to one-third of the colony as in the present species. They are distinguished by having 5 or 6 coils of the vas deferens and relatively narrow gut loops. *L. variegatus* has larger spicules (to 0.08mm) with pointed rays. *L. rigidus* resembles the present species in its superficial bladder cell layer and spicules with chisel-shaped and conical rays but is distinguished by its deeper common cloacal spaces and fewer vas deferens coils. *L. placidus* has spicules of similar form, but they are larger and distributed evenly throughout. *L. rufus* has a more conspicuous bladder cell layer, fewer vas deferens coils, and larger spicules than the present species.

Leptoclinides sulawesii
Monniot & Monniot, 1996
(Figs 38,160E)

Leptoclinides sulawesii Monniot & Monniot, 1996: 110.

NEW RECORD. Western Australia (Dongara, WAM 106.93). New South Wales (Twofold Bay, QM G308493).

PREVIOUSLY RECORDED. Indonesia (north Sulawesi – Monniot & Monniot, 1996). Palau Is (Monniot & Monniot, 1996).

COLONY. One of the newly recorded colonies is tough and surrounds a kelp stalk (WAM 106.93). The other is more gelatinous. Both are up to 3mm thick and have firm translucent test with spicules evenly distributed in the surface gradually reducing in number toward the base. A thin layer of bladder cells is on the surface, although these often are inconspicuous. The upper surface has circular elevations, each with a central common cloacal aperture. A large posterior abdominal common cloacal cavity is beneath each of the cloacal apertures and penetrates between zooids around the periphery of the primary cavity. Zooids are present in the flat areas between the surface mounds as well as over the common cloacal cavities. Five spicule-filled lobes around each atrial aperture are evident in the roof of the common cloacal cavity. Spicules are to 0.075mm diameter and have 7–9 conical, pointed and sometimes chisel-shaped rays in optical transverse section. The ray length/spicule diameter ratio is about 0.3.

Western Pacific colonies (Monniot & Monniot, 1996) were orange in life, fading to red in preservative. Colour of the newly recorded material is not known.

ZOOIDS. Zooids are small with a relatively long posteriorly oriented atrial siphon with 5 points around its rim. Branchial lobes are reduced to 6 small knobs around the rim of the aperture. About 10 stigmata are in the anterior row. The gut forms a more or less vertical loop, the distal part not being appreciably bent ventrally. Monniot & Monniot (1996) reported 3 to 5 male follicles, 7 coils of the vas deferens, a larvae with a trunk 0.085mm long with a tail wound halfway around it, 2 broad lateral ampullae each side of the median adhesive organs and dorsal and ventral epidermal ampullae.

REMARKS. Western Pacific colonies (Monniot & Monniot, 1996) and the form and distribution of their spicules are the same as in the newly recorded material, which extends the previously known tropical range well down the western and eastern coasts of Australia.

The temperate species *L. imperfectus* has similar colonies but more numerous, shorter and often truncated spicule rays and *L. compactus* has similar orange colonies but more spicule rays than the present species.

Leptoclinides umbrosus sp. nov.
(Figs 39,158D; Pl. 4C)

TYPE LOCALITY. Queensland (Heron I., eastern end of reef, low tide, coll. P.Kott 03.09.94, syntypes QM G308279; Gorgonia Pools, low tide, coll. P.Kott 06.09.94, syntypes QM G308283).

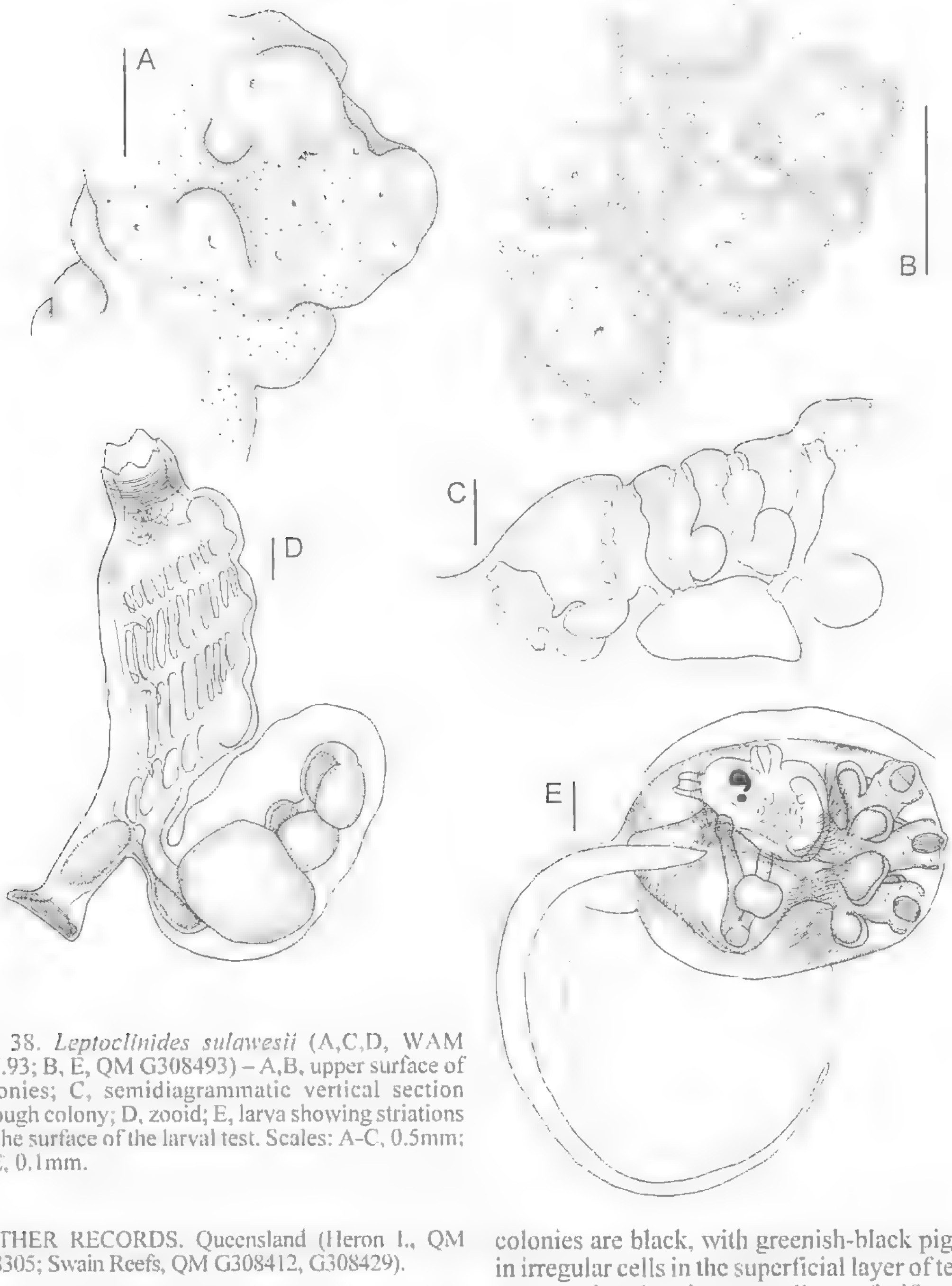


FIG. 38. *Leptoclinides sulawesii* (A,C,D, WAM 106.93; B, E, QM G308493) – A,B, upper surface of colonies; C, semidiagrammatic vertical section through colony; D, zooid; E, larva showing striations on the surface of the larval test. Scales: A-C, 0.5mm; D,E, 0.1mm.

FURTHER RECORDS. Queensland (Heron I., QM G308305; Swain Reefs, QM G308412, G308429).

COLONY. Irregular, spreading colonies with rounded margins are black and jelly-like with a thick, translucent superficial layer of bladder cells. Beneath the bladder cells white spicules are in moderate concentrations but are sparse in the lower half of the colony. Sometimes they are present mainly around the zooids. In life the colonies are black, with greenish-black pigment in irregular cells in the superficial layer of test. In preservative the pigment cells are fusiform and some tan or brown ones are mixed with the black. The concentrations of spicules affect the colour of colonies, which become grey where spicules are most crowded. The branchial openings are surrounded by pigmented test. Spicules do not project up into the pigmented bladder cell layer

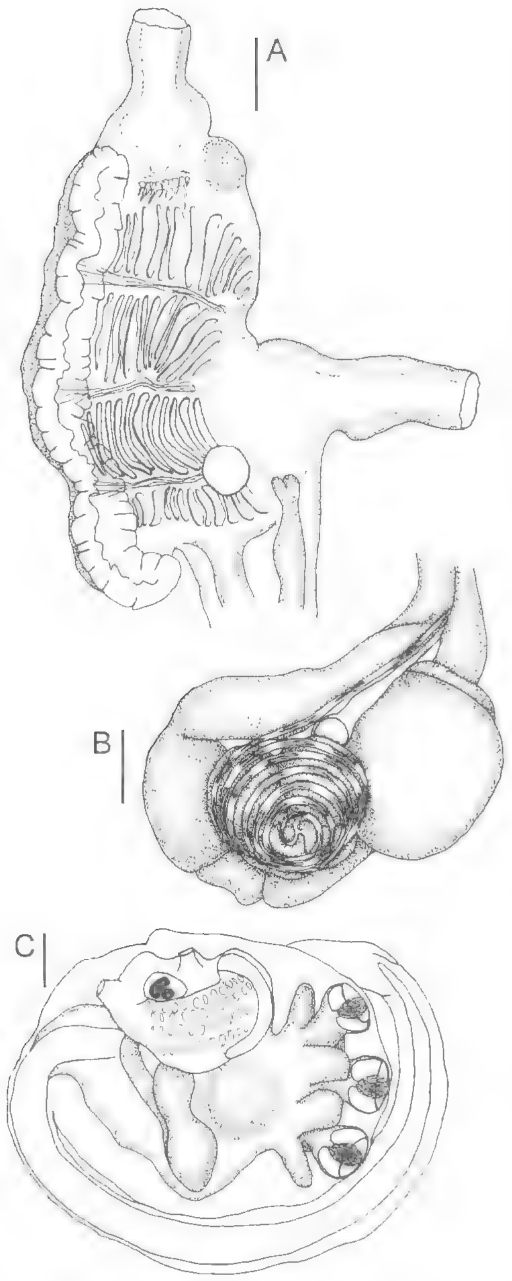


FIG. 39. *Leptoclinides umbrosus* sp. nov. (QM G308279) – A, thorax; B, abdomen; C, larva. Scales: 0.1mm.

around the branchial apertures, nor down into the branchial siphons.

Spicules are large, stellate, to 0.08mm in diameter with relatively short conical rays, 13–15 in optical transverse section, sometimes set in concavities in the central mass and well separated from one another, but in other spicules they are crowded together.

ZOOIDS. Zooids are about 1.5mm long, the thorax being about twice the length of the abdomen. Lobes were not detected around the branchial aperture which is on a long siphon with a pronounced chamber at its base into which the forward pointing branchial tentacles are projected in preserved specimens. The atrial siphon also is long and narrow, projecting posteriorly to open into the common cloacal cavity. Neither branchial nor atrial apertures have lobes in the present specimens. Fourteen oval stigmata are in the anterior row of the branchial sac, reducing to 12 in the posterior row. A large circular lateral organ is in on each side near the base of the atrial siphon. The gut forms a short loop, its posterior pyloric part being bent ventrally at right angles to the proximal part of the loop. Two short vascular appendages project from the ventral concavity of the abdomen. The testis has 4 or 5 follicles and the vas deferens winds 6 times around them.

Larvae, present in the basal test of specimens collected in September (QM G308279, G308283) have an almost spherical trunk 0.65mm long, with the tail wound two-thirds of the way around it. Two pairs of lateral ampullae and median dorsal and ventral ampullae surround the 3 large antero-median adhesive organs at the anterior end of the trunk. The lateral ampullae seem to develop late and sometimes are not present, the short thick stalks of the adhesive organs being set in a concavity at the anterior end of the trunk. Occasionally 4 adhesive organs are present. Adult organs (branchial sac, gut loop and branchial and atrial siphons) are well formed. The branchial sac has 4 rows of stigmata.

REMARKS. The absence of white spicules associated with the opening of the branchial siphons is unusual. Spicules are not present in the thick surface bladder cell layer of the related *L. rufus* (which also has a conspicuous smooth superficial layer of bladder cells). The present species differs from *L. rufus* in its black (rather than black, orange and white marbled pattern) and translucent appearance and the short conical spicule rays set in the central mass of each spicule. *L, rigidus* (which also has a superficial bladder cell layer, and spicules absent or sparse in the basal test) has smaller spicules (to 0.05mm diameter) with fewer rays (7–9) in optical transverse section. The spicules, with their short conical points set in concavities in the central mass, resemble those of *D. vahatuio* Monniot & Monniot, 1987.

Leptoclinides variegatus sp. nov.
(Figs. 40, 159B; Pl. 4D)

Leptoclinides rufus: Kott, 1962, 286 (part, colonies from S.A. and Vic.); 1972a: 16 (part)
Leptoclinides reticulatus: Kott, 1972a: 18; 1972b: 180; 1975: 8 (part, see also *Polysyncraton tasmanense*, below).

TYPE LOCALITY. South Australia (Topgallant I., in caves 7m, coll. N. Holmes 10.4.83 photo index PE0033, holotype QM GH2426; paratype QM GH2428).

FURTHER RECORDS. South Australia (northern Great Australian Bight – SAM E2697 Kott, 1975; Investigator Strait – MV F68823 Kott, 1972b; St Vincent Gulf – SAM E2672 Kott, 1972a; Spencer Gulf – SAM E2628 E2835 Kott,1972a).

COLONY. Colonies are tough, leathery, flat sheets with a smooth, even upper surface. Common cloacal apertures, sessile, sometimes very large with frilled rims and up to 15 radial spicule-filled ribs around the aperture, are fairly evenly spaced around the margins of the colony. In living colonies, spindle or irregular shaped pigment cells mixed with spicules and bladder cells in the superficial layer of test create the marbled pattern of orange and black pigment or orange and green. This pattern persists for varying times in preservative. The branchial apertures have 2–6 small clumps of 2 or 3 spicules in the centre of each opening. The colour pattern is not related to zooid distribution, and branchial openings are in both orange and grey parts of the colony. The cloacal cavity is a shallow horizontal space at posterior abdominal or oesophageal level and zooids are held tightly in the test. Large spicules (to 0.09mm diameter) with 11–13 conical, pointed or chisel-shaped rays are present, but not crowded, in the upper half of the colony, including the superficial layer of test and the floor of the common cloacal cavity, and are absent or sparse in the basal half.

One of the specimens (SAM E2672) which Kott (1972a) had assigned to *L. rufus* has brownish-red zooids in preservative and the label stains brownish-pink.

ZOOIDS. Zooids are moderately long, to 2mm overall. Lobes were not detected around the rim of the branchial aperture. Short postero-laterally oriented atrial siphons from the postero-dorsal corner of the thoraces have 5 points around their rims where they open into the posterior abdominal cloacal cavity. A large (to 0.1mm diameter) saucer-shaped lateral organ is on each side of the posterior half of the thorax. Stigmata are in 4 rows of up to 12 (in the anterior row). The gut forms a simple rather rounded loop. The stomach is small and almost spherical, the duodenum is long and slightly expanded distally, and a small rounded posterior stomach is in the pole of the gut loop. Gonads were not detected in the type material but are in previously recorded material (Kott, 1972a, 1975). The testes have 4–9 follicles surrounded by 5 coils of the vas deferens. Zooids of one of the colonies (SAM E2672) have a rudimentary brood pouch containing a small loop of the oviduct projecting from the postero-dorsal corner of the thorax. However, larvae, present in the same colony (collected in December), were free in the test. They have a trunk 0.6mm long with 4 broad ampulla on each side of the 3 antero-median adhesive organs and a horizontal ampulla on the left in the vicinity of the larval waist. Zooids were not readily removed from the test.

REMARKS. The marble pattern of the colonies resembles that of the tropical *L. rufus*. However, the rare giant spicules of the latter species are not present in *L. variegatus*, which is also distinguished by having spicules in the superficial bladder cell layer and by the occasional chisel-shaped spicule rays. Further, the zooids are very much smaller than those of *L. rufus*. The presence of a brood pouch, if confirmed would be a distinctive character, found also in the tropical *L. brandi*.

Kott (1962, 1972a,b, 1975) assigned specimens of the present species to *L. reticulatus* and *L. rufus* according to the shape of the pigment cells — oval in *L. rufus*; branched and fusiform in *L. reticulatus*. However, the small irregular and very variable pigment cells in *L. variegatus* are not a reliable character. Kott also overlooked the facts that *L. rufus* is tropical and the present species temperate and that *L. reticulatus* is a species of *Didemnum* (<*D. jedanense*).

The thin sheet-like colonies and small zooids resemble sympatric *L. exiguus*, which usually has a superficial bladder cell layer occasionally with spicules mixed in it, as in the present species. However, zooids of *L. exiguus* are arranged in double rows around spicule-free areas of test that extend from surface to basal test interrupting the extensive posterior-abdominal cloacal cavity and resulting in raised areas on the colony surface that contrast with the smooth even surface of the present species. *L. maculatus* is another sympatric species that resembles the present one — having relatively small zooids, oesophageal common cloacal cavities and the otherwise smooth, even, colony surface slightly depressed over deep, circular, primary common cloacal

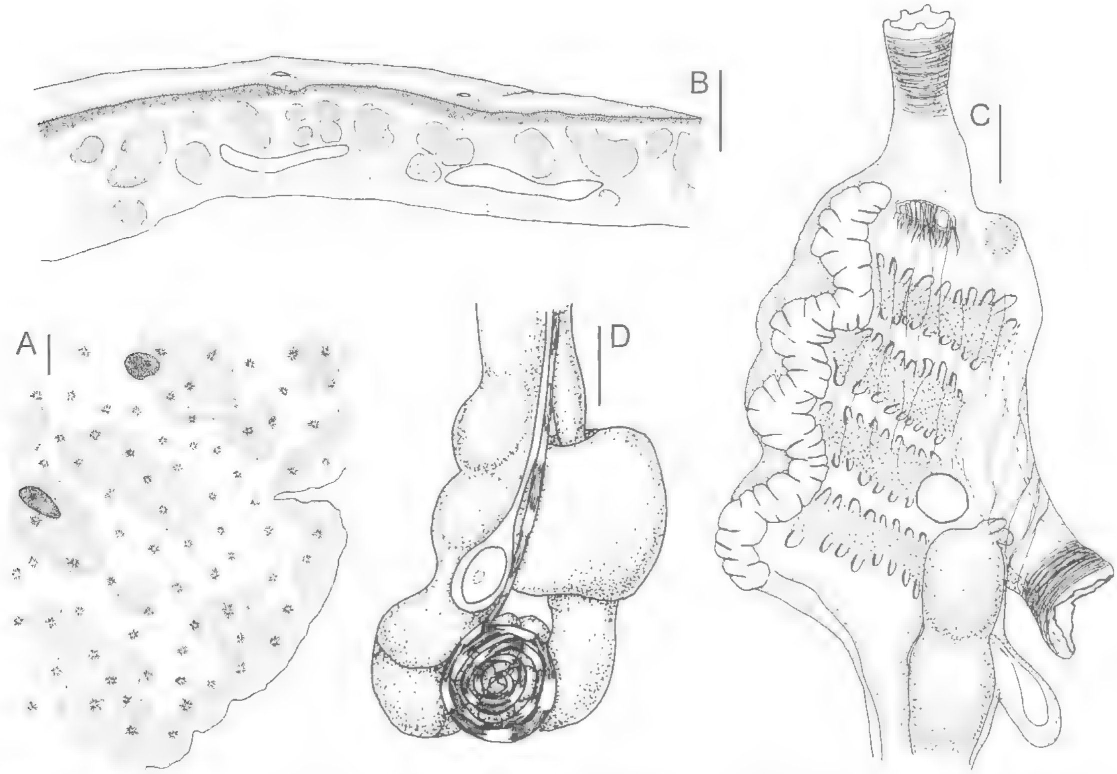


FIG. 40. *Leptoclinides variegatus* sp. nov. (A,B, QM GH2428; C,D SAM E2672) – A, colony from above showing marbled pattern and arrangement of branchial and common cloacal apertures; B, semidiagrammatic vertical section through colony showing some common cloacal apertures on the surface, common cloacal canals and spicules most crowded at surface; C, thorax showing parietal longitudinal muscles and possibly a rudimentary brood pouch; D, abdomen. Scales: A,B, 1.0mm; C,D, 0.1mm.

canals. Its spicules are smaller (up to 0.07mm) and have slightly fewer rays than the present species. *L. compactus* also has some spicules in its superficial bladder cell layer, but its spicules are smaller and its posterior abdominal cavities more extensive than in the present species. *L. placidus* from the east coast of Australia has a similar superficial bladder cell layer but its spicules are more crowded in the lower half of the colony than in the present species.

The colour of the colony, and the common cloacal systems with apertures around the margins of the colony are similar to *L. marmoreus* Brewin, 1956 from the Chatham Is (New Zealand). The species may be related, but the New Zealand species has smaller spicules to 0.045mm diameter (Millar, 1982).

The specimen lot referred to *L. reticulatus* by Kott (1975) contains a specimen of the present species, and a more opaque colony, with spicules more crowded throughout was found to be *Polysyncraton tegetum*.

Leptoclinides volvus Kott, 1975
(Figs. 41, 157-I; Pl. 4E)

Leptoclinides volvus Kott, 1975: 8; 1998: 87.

NEW RECORDS. South Australia (Nuyts Archipelago, SAM E2474 E2598, QM GH926, G300900).

PREVIOUSLY RECORDED. South Australia (northern Great Australian Bight – holotype SAM E1034, paratypes SAM E1033, QM G7511 Kott, 1975).

COLONY. Colonies are circular to irregular, slightly flattened heads to 5cm in diameter, narrowing to a thick fleshy stalk up to 5cm long, 3cm wide and often flattened and almost ribbon-like or short and stumpy. Basally the stalk appears frayed where it was attached to the substrate. Conspicuous blister-like protuberances separated from one another by surface depressions over the branching cloacal canals create an irregular open network on the surface of the colony. In preservative, the blister-like

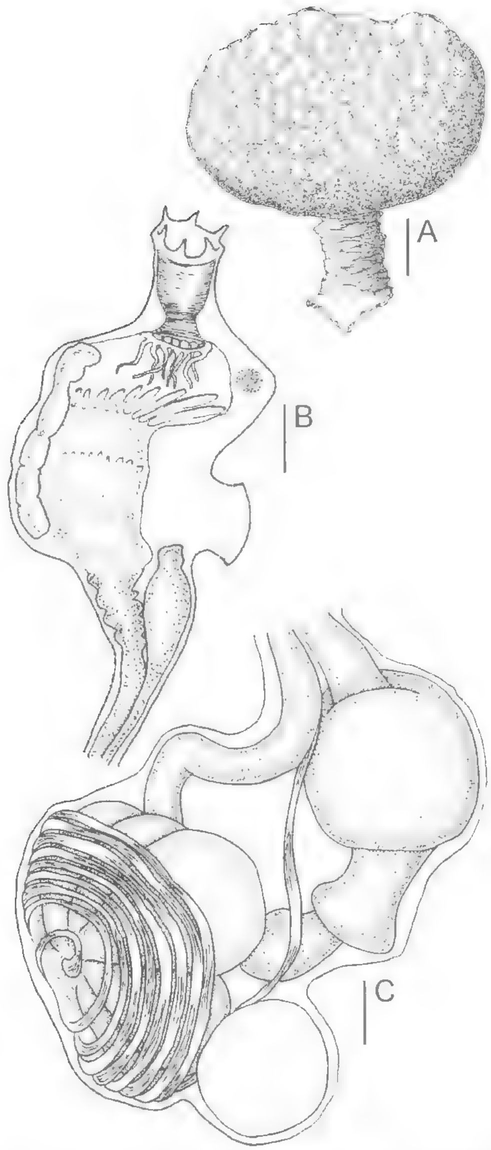


FIG. 41. *Leptoclinides volvus* (A,C, SAM E2474; B, QM GH926) – A, colony showing zooid openings along each side of depressions over primary cloacal canals; B, thorax; C, abdomen. Scales. A, 1.0cm; B,C, 0.2mm.

protuberances are packed with masses of brownish pigment cells. In some colonies minute patches of debris in the central test are surrounded by these brownish pigment cells to form patches in the test. Generally the colonies are some shade of blue or blue-purple (SAM E2598) or grey (QM GH926) with bluish zooids seen through the translucent test. Several common cloacal apertures are at the junctions of common cloacal canals on the upper free surface of the head of the colony. Double rows of zooids are along the sides of the cloacal canals, which are at oesophageal level and the circular atrial openings of the zooids can be seen in the oesophageal common cloacal canals. A thick superficial layer of bladder cells is on the outside of both head and stalk.

Spicules are in clouds at oesophageal level, and postero-abdominally. They often are overlooked, and sometimes are not present. They are minute, <0.013mm diameter. Some are stellate with 9–11 rather blunt but quite long conical rays, while others are globular with flat-tipped rays.

ZOOIDS. Zooids are small, the thorax and abdomen about 2mm long, including a relatively long oesophageal neck. The surface of both thorax and abdomen is covered with rounded projecting columnar ectodermal cells. The branchial aperture is on a distinct siphon with 6 pointed lobes around the rim. The atrial opening, on a very short siphon with a short sphincter muscle, is directed horizontally from the postero-dorsal corner of the thorax. Nine or 10 long, oval stigmata are in the anterior row. The gut loop is short, and fairly wide with the usual long duodenum expanded distally, and a posterior stomach in the pole of the loop. Gonads are posterior to the gut loop. They consist of 8–10 large male follicles crowded into a circle (rather than being in a single ring), more or less parallel to one another, joining the vas deferens at their posterior end. The 8 coils of the vas deferens form a cap over the posterior (outer) half of the testis. One large egg projects from the side of the zooid to the right of the testis. Specimens collected in March (QM GH926, SAM E2474) have well-developed male and female organs. One specimen (SAM E2598) appears to be a juvenile. Larvae are not known.

REMARKS. The stalked colonies are unusual, most *Leptoclinides* spp. being irregular encrusting forms. As Kott (1975) observed, the colonies resemble those of *L. fungiformis*, but *L. volvus* has longer and less pointed spicule rays, a less extensive cloacal cavity (lacking a posterior abdominal component), a short atrial siphon and long branchial siphon (in *L. fungiformis* the atrial siphons are long and the branchial apertures almost sessile), a superficial layer of bladder cells, spicules absent from the central test and the stalk and zooids arranged along each side of the common cloacal canals to form a surface pattern. In the present species oesophageal cloacal canals

are a unique feature contrasting with the extensive posterior abdominal cavities in *L. fungiformis* and most other *Leptoclinides* spp. The colonies resemble those of *Polysyncraton pedunculatum*, which, however, are softer and more gelatinous, lack spicules, have an open atrial aperture, smaller circular cloacal canals and half the number of vas deferens coils of the present species.

Genus **Polysyncraton** Nott, 1892

TYPE SPECIES. *Polysyncraton paradoxum* Nott, 1892.

Species of this genus have 2 or more testis follicles, a loosely coiled vas deferens, 4 rows of stigmata, a wide, sessile atrial aperture often with a muscular tongue (the tip bifid or forked and deeply divided) from the anterior rim, and usually a retractor muscle. The thorax is relatively large with 9 or more stigmata per row. The duodenum opens into a short but broad section of mid-gut (rather than a distinct posterior stomach) which expands to join the wide proximal half of the rectum in the pole of the gut loop. The distal half of the rectum is a narrow cylindrical tube. The vas deferens has loose and often relatively few coils. In 10 species examined in this study in which ovary and testis are present, the ovary is between the outer coil of the vas deferens and the inner coils. As the egg develops and projects out from the abdomen, the outer coil of the vas deferens around its outer surface is displaced and the inner coils are distorted (especially *P. magnetae*, *P. pulchrum*). In *P. arafurensis*, *P. glaucum*, *P. meandratum* a single colony has some zooids with the egg developing outside the vas deferens coils — although other colonies of these species do have the egg developing between the outer coil and the inner coils. Only in *P. oceanium* were developing eggs found always outside the vas deferens coils. It is probable that the exact location of the ovary in relation to vas deferens coils is random, affected by the looseness of the coils.

The body wall of the adult zooids often has projecting columnar epithelial cells, especially around the anterior part of the thorax at the base of the branchial siphon. However, they also occur over the whole thorax and often over the whole zooid (see Glossary).

The lateral organ on each side of the thorax ventral to the atrial aperture, is a small saucer to cup-shaped depression in the parietal body wall. It is smaller and deeper than the lateral organ in *Leptoclinides*.

Larvae often are large and yolky, the trunk usually being more than 0.5mm long, often up to 0.75mm or more. Usually numerous (8 pairs or more) lateral ampullae surround the 3 antero-median adhesive organs. In well advanced specimens of most known larvae a finger-like epidermal ampulla, possibly a rudimentary stolonic vessel, projects vertically or backwards and horizontally from the waist of the left side of the trunk (in the vicinity of the gut loop) into the larval test (as in *Leptoclinides*, *Didemnum* and some *Trididemnum)*. Often a blastozooid is developing in the trunk as well as the oozooid. Sometimes 2 blastozooids occur (2 thoracic and 2 abdominal buds — e.g. *P. arafurensis*), although this is unusual in this and other genera, except *Lissoclinum*, *Diplosoma* and *Clitella.* Four rows of stigmata are in the larval oozooids of all larvae examined in this work as well as in the blastozooids. Monniot (1993) shows only 3 rows of stigmata in the oozooids of the larvae she has figured, although 4 are shown in *P. purou* Monniot & Monniot, 1987. Adult organs (branchial sac and gut) are not always well advanced in the tailed larvae, although they are by the time that blastozooids are present.

The relatively small zooids, large sessile atrial apertures exposing much of the branchial sac directly to the cloacal cavity, 4 rows of stigmata and coiled vas deferens, suggest a relationship with *Didemnum*. In the absence of mature testes or larvae, some difficulty is encountered in separating *Polysyncraton* and *Didemnum*, for many characters which occur frequently (but not always) in *Polysyncraton* are not exclusive to it, sometimes also being found in *Didemnum*. For instance, in the present material:

1. A retractor muscle (as in *Didemnum* and *Trididemnum*) is absent only from *P. palliolum* and *P. poro* Monniot & Monniot, 1987.

2. *P. rugosum* Monniot, 1993, *P. aspiculatum* (Tokioka, 1953) and *P. recurvatum* are known to have as few as 4 lateral ampullae on each side in the larval trunk and *P. pontoniae* is reported (Monniot & Monniot, 1987) to have 5. Although most *Didemnum* have 3 or 4, some species have 5 or more (like the majority of *Polysyncraton* species).

3. Among *Polysyncraton* species discussed below a long anterior atrial lip is present in all except *P. multipapillae* Monniot, 1993 and *P. recurvatum* Sluiter, 1909, while in *Didemnum* an atrial lip sometimes occurs but is relatively short.

4. The number of vas deferens coils usually is less than 8 in *Polysyncraton* — but is not always more than 8 in *Didemnum*.

5. *Polysyncraton* can be confused with *Didemnum* if only 2 testis follicles are present, as occasionally a *Didemnum* sp. has a 2-lobed testis.

Generally, a combination of characters can be used to distinguish *Polysyncraton* (as in *P. oceanium*), but even that is not always satisfactory, as the atrial tongue, large larvae with 8 or more lateral ampullae on each side and a blastozooid sometimes occur together in *Didemnum* (see *D. arancium, D. caesium, D. multispirale* and *D. precocinum*).

Despite the difficulty sometimes encountered in distinguishing between them, *Polysyncraton* zooids do differ from *Didemnum* in their large thoraces which seldom have fewer than 10 stigmata per row; long cylindrical distal part of the rectum; the loose coils of the vas deferens, often with the outer coil displaced by the ovary; the 4 rows of stigmata in the larval pharynx; and often the slow development of adult organs such as gut and pharynx. Monniot's (1995) view that they are congeneric is not supported by the present study (see, also, *Didemnum*).

In *Polysyncraton* the divided testis and 4 rows of stigmata in the larval oozooid are more like *Leptoclinides*, from which it is readily distinguished by its smaller zooids, absence of an atrial siphon, large sessile atrial apertures usually with a long, forked atrial tongue, a retractor muscle in most species, a broad expanding mid-gut lacking a constriction at its junction with the rectum, loose coils of the vas deferens, larval blastozooids and often numerous larval lateral ampullae.

Polysyncraton also differs from all other didemnid genera except *Leptoclinides*, in that species in obligate symbioses with *Prochloron* or other plant cells are known in one species only. *Prochloron*, apparently in a non-obligate symbiosis, is present on the surface of *P. scobinum* and *P. magnetae* Hastings, 1931. *P. multipapillae* Monniot, 1993 is the only other species of the genus reported to contain symbiotic plant cells — although it is not known whether or not these are *Prochloron* — being recorded merely as unicellular (Monniot, 1993). Monniot (1993) also referred to a rastrum, but the organ figured (Monniot, 1993, Fig. 3D) is a ventral projection of the larval haemocoel and does not in any way resemble a rastrum. The rastrum, for transfer of symbiotic cells from the host organism to the next generation (Kott, 1980, 1981, 1982a,b), has been recorded only in *Prochloron-Diplosoma* symbioses. It is a dorsal outgrowth at the base of the tail, in the vicinity of the developing common cloacal cavity. The role of the organ referred to by Monniot (1993) is not known — but, since it lies beneath the insertion of the tail into the trunk and is not in the vicinity of the developing common cloaca, it probably is not for symbiont transfer.

With the exception of Sluiter's (1909) report on the *Siboga* collection, little work had been done on this genus in, and few species were known from, the tropical western Pacific until 1987 (Monniot & Monniot, 1987, 1996 and Monniot, 1993). As *Polysyncraton* is not known to contain species in symbiosis with green plant cells it was not reported on by Kott (1980, 1981).

Polysyncraton is well represented in Australian waters, although it is not as diverse as *Didemnum*. It is commonly encountered in both tropical and temperate waters. Newly reported from Australian waters are 3 of the 4 species described from French Polynesia (Monniot & Monniot, 1987), and 4 of the further 6 recorded from New Caledonia (Monniot, 1993).

KEY TO THE SPECIES OF *POLYSYNCRATON* FROM AUSTRALIAN WATERS

1. Spicules sparse in, or absent from, all or appreciable parts of the colony 2
   Spicules not sparse in, or absent from, appreciable parts of the colony 16
2. Colony completely aspicular . *P. pedunculatum* sp. nov.
   Colony not completely aspicular 3
3. Superficial bladder cell layer conspicuous 4
   Superficial bladder cell layer absent or inconspicuous . 9
4. Spicules in patches beneath superficial bladder cell layer 5
   Spicules in continuous layer beneath superficial bladder cell layer. . . . . *P. rica* sp. nov.
5. Spicules all stellate, with 13 – 15 short conical rays in optical transverse section . . . . *P. otuetue*
   Spicules not all stellate, and with more than 15 rays in optical transverse section 6
6. Spicules often with pointed rays, to more than 0.03mm diameter. 7
   Spicules seldom with pointed rays, not more than 0.03mm in diameter. . . . . *P. dromide* sp. nov.
7. Spicule rays more than 20 in optical transverse section . . . . *P. meandratum*
   Spicule rays not more than 20 in optical transverse section 8
8. Common cloacal cavities circular canals. . . . *P. purou*
   Common cloacal cavities horizontal spaces . . . . *P. robustum* sp. nov.

9. Spicules all burr-like with fine uniform rod or needle-like rays . . . . *P. pulchrum* sp. nov.
Spicules not all burr-like with fine uniform rod or needle-like rays 10
10. Spicules stellate, rays mostly conical 11
Spicules not only stellate, rays flat and/or round-tipped as well as conical 13
11. Spicules to 0.08mm or more diameter, ray length/spicule diameter ratio about 0.25 12
Spicules not more than 0.06mm diameter, ray length/spicule diameter ratio 0.4 . . . . . . *P. echinatum* sp. nov.
12. Colonies upright, entire or subdivided into 2 or 3 lobes, each with a single terminal common cloacal opening . . . . *P. rugosum*
Colonies sheet-like, not upright lobes with terminal common cloacal apertures . . . . . *P. scobinum* sp. nov.
13. Spicules with 20 or more rays in optical transverse section 14
Spicules with fewer than 20 rays in optical transverse section 15
14. Spicules sometimes hollow; vesicles in colony surface . . . . *P. circulum*
Spicules never hollow; no vesicles in colony surface . . . . *P. multiforme* sp. nov.
15. Spicules include some with regular conical rays; spicules crowded at thorax level . . . . . . *P. dentatum* sp. nov.
Spicules never with regular conical rays; spicules in a single layer at the surface . . . . . *P. flammeum* sp. nov.
16. Spicules to 0.07mm diameter or more 17
Spicules less than 0.07mm diameter 28
17. Spicules all stellate; spicule rays all conical, pointed, or truncated or chisel-shaped 18
Spicules not all stellate; spicule rays flat- or blunt-tipped or rounded 26
18. Cloacal systems an isolated group of zooids around a central common cloacal aperture . . . *P. glaucum* sp. nov.
Cloacal system not an isolated group of zooids around a central common cloacal aperture 19
19. Ray length/spicule diameter ratio never more than 0.2 . . . . *P. infundibulum* sp. nov.
Ray length/spicule diameter ratio usually more than 0.2 20
20. Spicules with up to 9 rays in optical transverse section; vesicles surround branchial apertures in surface test . . . . *P. sideris* sp. nov.
Spicules with up to 11 or more rays in optical transverse section; vesicles do not surround branchial apertures in surface test 21
21. Spicule diameter to 0.1mm or more 23
Spicules diameter less than 0.1mm 22
22. Branchial apertures along each side of deep primary cloacal canals . . . . *P. pseudorugosum*
Branchial apertures not along each side of deep primary cloacal canals . . . . *P. arafurensis*
23. Zooids dark green in long-term preservative . . . . *P. tasmanense* sp. nov.
Zooids not dark green in long-term preservative . . . 24
24. Spicule diameter to more than 0.1mm 25
Spicule diameter to 0.1mm . . . . . . *P. regulum* sp. nov.
25. Spicules sometimes have chisel-shaped tips . . . . *P. tegetum* sp. nov.
Spicules never have chisel-shaped tips . *P. lodix* sp. nov.
26. Spicules include some conspicuously stellate ones with few conical rays . . . . *P. tenuicutis* sp. nov.
Spicules do not include conspicuously stellate ones with few conical rays 27
27. Spicule rays long, often flattened and tongue-shaped . . . . *P. pontoniae*
Spicule rays short, never flattened and tongue-shaped . . . . *P. scorteum* sp. nov.
28. Spicules include stellate ones with conical rays 30
Spicules do not include stellate ones with conical rays . 29
29. Pigment cells present in surface test; tropical species . . . . *P. rugosum*
Pigment cells not present in surface test; temperate species . . . . *P. discoides* sp. nov.
30. Retractor muscle present 31
Retractor muscle not present 35
31. Spicules to 0.05mm diameter or more 32
Spicules not more than 0.04mm diameter 34
32. Spicule rays to 15 or more in optical transverse section . . . . *P. oceanium* sp. nov.
Spicule rays less than 15 in optical transverse section . 33
33. Black squamous epithelium present; no dense rippled colony base . . . . *P. orbiculum*
Black squamous epithelium not present; with dense, rippled colony base . . . . *P. millepore*
34. Spicules globular and stellate . . . . *P. magnetae*
Spicules only stellate . . . . *P. papyrus* sp. nov.
35. Spicules with 17 to 19 long pointed rays in optical transverse section . . . . *P. palliolum* sp. nov.
Spicules with 7 – 9 rays in optical transverse section . . . . *P. rubitapum* sp. nov.

Species reported from adjacent water but not yet recorded from Australia are:

Polysyncraton aspiculatum (Tokioka, 1953) from Japan has 5–12 male follicles, and up to 4 lateral ampullae on each side of the long larval trunk. It lacks spicules, but unlike the stalked *P. pedunculatum* (which also is aspicular) it is a sessile colony. Specimens wrongly assigned to this species by Kott (1962) are *P. purou* from Mackay and a related but distinct species (*P. robustum*) from Rottnest I. The Japanese species resembles *P. magnilarvum* Millar, 1962 from South Africa only in the size of the larval trunk (see *P. robustum*). *Polysyncraton aspiculatum*, Kott, 1975 (<*P. pedunculatum*) is discussed below.

Polysyncraton chondrilla (Michaelsen, 1924) from the subantarctic islands of New Zealand (Millar, 1982) forms soft, fleshy, upright colonies to 8cm high, narrow basally and undivided, with terminal common aperture. The small (to 0.035mm diameter) spicules are principally in a layer in the surface test but occasionally in other parts as well. One colony is known to be aspicular (Colville Channel: Michaelsen, 1924). Zooids have 4 or 5 male follicles and 4 coils of the vas deferens. The species resembles *P. pedunculatum* which also is aspicular but has about 8 male follicles.

Polysyncraton jugosum (Herdman & Riddell, 1913), which Kott (1962) thought to be synonymous with *P.*

chondrilla, has similar spicules, stellate with 7–9 rays in optical transverse section. It is distinguished by its 8 male follicles.

Polysyncraton fuscum Nott, 1892 from Auckland, was proposed (Michaelsen, 1924), and generally accepted (Brewin, 1957; Millar, 1982), as a junior synonym of *P. paradoxum* Nott, 1892 (also from Auckland). However, although the gonads are similar, the spicule distribution is different and *P. fuscum* had a retractor muscle which has not been reported in *P. paradoxum*. In *P. paradoxum* spicules are throughout the colony but in *P. fuscum* they are present only around the zooids. Nott (1892) refers to a transparent colourless outer hyaline layer of test and large zooids which, with the location of the spicules, resemble the tropical *P. purou*, *P. otuetue* and *P. meandratum*. Of these 3 tropical species, only *P. meandratum* has relatively small burr-like spicules that could be like those of *P. fuscum*. Material from the type locality, Auckland Harbour, is needed to establish the form of the spicules and the exact relationships of this species. Tropical species are known to occur in Auckland Harbour.

Polysyncraton lithostrotum (Brewin, 1956) was recorded only from sub-antarctic locations (Brewin, 1956, 1958; Millar, 1982) but now is known from the Coromandel Peninsula (QM G300968, G300989). The newly recorded specimens, like Brewin's (1956) type material, are orange. The species is characterised by its surface marked off into polygonal areas, each a separate system, with a central cloacal aperture, the testis divided into 2 follicles, a narrow atrial tongue of various lengths, a small retractor muscle (sometimes not detected), and spicules to about 0.06mm diameter with 9–11 short, blunt, almost globular rays. The large larvae from QM G300989, with the trunk about 0.7mm long, have about 35 short, round-tipped ectodermal ampullae around the anterior end of the trunk giving it a scalloped appearance. The 3 antero-median adhesive organs are small with short cylindrical stalks. Ocellus and otolith are present. Neither adult organs nor blastozooids have been detected. Brewin's (1956) record of a larva 1.5mm long appears to include the tail. *P. glaucum* and *P. multiforme* as well as *P. pavimentum* Monniot, 1993 (>*P. lithostrotum*: Monniot, 1993, see below) are tropical species with similar isolated systems but different spicules.

Polysyncraton mortenseni (Michaelsen, 1924) from New Zealand, has large (about 0.085mm diameter) spicules with round-tipped rays, 2 or 3 testis follicles and 6 coils of the vas deferens. Specimens from Tasmania were wrongly assigned to *P. mortenseni* by Kott (1954, 1962). *P. tasmanense*, *Leptoclinides magnistellus* and *Trididemnum cristatum* are erected to accommodate them.

Polysyncraton multipapillae Monniot, 1993 from New Caledonia forms red-currant coloured colonies which become greenish in formalin. Globular spicules (to 0.03mm diameter with thick flat-tipped rays) are crowded throughout, and the colonies are brittle. Unicellular algae are in the common cloacal cavity and embedded in the surface test, but it is not known if these are pro- or eukaryotic; and the contribution made by these cells to the colour of the colonies has not been determined. The small zooids lack an atrial tongue. They have a retractor muscle, about 8 stigmata per row, about 5 testis follicles and 7 coils of the vas deferens. The larval trunk is about 2.0mm long, with 15–25 adhesive organs and about 15 ectodermal ampullae along each side of the adhesive organs. Restricted cloacal canals are at thorax level. Spicules resemble those of *P. meandratum* but have fewer rays, and are more evenly distributed. Larvae are unique, the number of adhesive organs being exceeded only by *Diplosoma multipapillatum* Kott, 1980 from Fiji. This is the only known species of *Polysyncraton* with possibly obligate green cell symbionts. Although the symbionts are transported on the larvae, Monniot's (1993) report of a rastrum is incorrect.

Polysyncraton nigropunctatum Sluiter, 1909 (ZMA TU838) from Indonesia, is the only species correctly assigned of the 5 he described in this genus — the others being *Leptoclinides* spp. The type colony is an irregular sheet to 2mm thick with zooids arranged in a row along each side of the circular canals beneath the slight surface depressions around zooid-free areas 2 to 3mm in maximum extent. Spicules to 0.04mm diameter, with short, strong conical rays, are in a layer beneath the surface bladder cell layer and on the base of the colony, but are absent between. Zooids are small, with 4 rows of 5 or 6 stigmata. Five male follicles have 5 coils of the vas deferens around them. Clearly defined black pigment spots are in the upper surface. The larval trunk is 0.6mm long and has an ocellus and an otolith, 4 rows of stigmata in the pharynx, 4 lateral ampullae on each side of the 3 antero-median adhesive organs, and an external lateral ampulla on the left side from the waist of the larval trunk. Blastozooids are not present.

Polysyncraton paradoxum Nott, 1892 from Auckland, New Zealand (see Millar, 1982) is an encrusting sheet. Although Nott (1892: 318) reported that the spicules were 'of fairly large size' Brewin (1957) refers to small (to 0.018mm diameter), burr-like spicules with many short blunt rays present throughout the colony. Seven–10 testis follicles have 4 coils of the vas deferens around them. Zooids have a long atrial tongue, but a retractor muscle is not reported. The species resembles *P. rugosum* Monniot, 1993 from New Caledonia and is distinguished from it only by having 4 rather than 3 coils of the vas deferens. *P. papyrus* also is similar but it does have a retractor muscle.

Polysyncraton paradoxum: Kott, 1954 is a specimen of *P. papyrus*, and *P. paradoxum*: Kott, 1972b is *Leptoclinides compactus*.

Polysyncraton paradoxum var. *mahenum* Michaelsen, 1920 from the Seychelles (<*P. mahenum*) has similar small spicules (to 0.018mm in diameter with 24 conical rays), and 2 coils of the vas deferens. It is unlikely to be a synonym of *P. paradoxum* which does not have a retractor muscle and has 4 coils of the vas deferens.

Polysyncraton pavimentum Monniot, 1993 from New Caledonia and *P. lithostrotum*: Monniot, 1993, from New Caledonia and the Coral Sea are conspecific. They have separate common cloacal systems (each with a central common cloacal aperture) isolated from one another by a ridge of test and stellate spicules (to 0.07mm diameter)

with 13–15 pointed conical rays in optical transverse section. Like *P. lithostrotum*, they both have 2 testis follicles and 6 coils of the vas deferens. The larva (see Monniot, 1993) has a large trunk (about 0.8mm long) with 3 small adhesive organs surrounded by a ring of about 24 finger-like lateral ampullae. The common cloacal systems resemble those of the tropical *P. glaucum*, *P. multiforme* and *P. lithostrotum* from New Zealand and subantarctic locations (see above). *P. lithostrotum* has a similar larva, large, without well developed adult organs but with more (35) ectodermal ampullae. The species are readily distinguished by their spicules, those of *P. pavimentum* and *P. multiforme* having conical pointed rays, *P. glaucum* rod-shaped rays and *P. lithostrotum* short, rounded (almost globular) rays.

Polysyncraton poro Monniot & Monniot, 1987 from French Polynesia, forms thin sheet-like colonies with large zooids (to 1.7mm long), a bifid atrial lip, spicules to 0.04mm diameter with very numerous short points, 3–7 testis follicles and 3 coils of the vas deferens. There is no retractor muscle. *P. circulum* and *P. meandratum* have similar spicules in the same size range but in both species they are confined to a surface and basal layer and are not crowded throughout as they are in the present species. The distended anterior parts of the thoraces (Monniot & Monniot, 1987: 84, figs 16A,B) probably result from narcotisation and should not be regarded as invariable or normal for zooids of this species.

Polysyncraton recurvatum (Sluiter, 1909), holotype ZMA TU474, an Indo-West Pacific species with a range from the West Indian Ocean to Fiji (see Kott, 1981), forms small red to pinkish colonies high in the intertidal region. Spicules are crowded throughout. The common cloacal cavity forms an open horizontal space at thorax level. Zooids lack an atrial lip, but have a retractor muscle projecting from the upper part of the oesophageal neck. Two testis follicles are surrounded by 5 coils of the vas deferens. The spicules (to 0.04mm diameter) are unusual in *Polysyncraton*, being globular with crowded, flat-ended, cylindrical rays. They resemble the spicules of *D. albopunctatum*, but are larger. *P. lithostrotum*, *P. millepore* and *P. oceanium* also have 2 (or 3) testis follicles, but have stellate spicules.

Polysyncraton rostrum Monniot, F. & Monniot, C., 1997 from Tanzania, forms large, thin, encrusting sheets with the surface raised in small, conical elevations, each with a terminal common cloacal aperture. Spicules are crowded throughout the colony. The thoracic common cloacal cavity has thoraces crossing it, each in a sheath of test and abdomina are embedded in the thick basal test. A small atrial tongue is present, there is no retractor muscle, and 5–6 testis follicles are surrounded by 2 coils of the vas deferens. Sixteen larval ectodermal ampullae surround the antero-median adhesive organs, a thoracic and an abdominal bud are present in the 0.6mm long larval trunk and the tail is wound three-quarters of the way around it. Spicules are to 0.04mm diameter, and are globular (with flat-tipped rays), or stellate (with 15–12 short conical rays in pentagonal bases). The spicules are identical to those of *P. oceanium* but the latter species has 6 coils of the vas deferens rather than 2 as in the present species. *P. multiforme* also has similar spicules but they are present only in a layer at the surface and the colonies are massive and branched.

Polysyncraton sagamiana (Tokioka, 1953) from Japan has stellate spicules to 0.037mm diameter with numerous, crowded, rounded rays, 6–8 testis follicles and 2 coils of the vas deferens. Colonies assigned to this species from the Palau Is (Tokioka, 1967) do not appear to be significantly different from the Japanese type material, although larvae are not known from either location. This species has similar spicules to *P. discoides* and *P. flammeum*. The atrial tongue and spicules crowded through the colony, distinguish it from the latter species. Except for the lesser number of vas deferens coils, characters distinguishing the species from *P. discoides* are not identified but although *P. sagamiana* may cross the tropics the latter species appears to be a temperate one.

Polysyncraton arafurensis Tokioka, 1952 (Figs 42A, 163E)

Didemnum (Polysyncraton) arafurensis Tokioka, 1952: 91.

NEW RECORDS. Western Australia (Dongara, WAM 108.93). Queensland (Heron I., QM G302266).

PREVIOUSLY RECORDED. Arafura Sea (Tokioka, 1952).

COLONY. Newly recorded colonies are particularly extensive, thin, hard sheets, about 3–4mm thick, with spicules crowded throughout. Spicules are in the surface of the colony and a spicule-free superficial layer is not present. A few large sessile common cloacal openings, each with a slightly gathered rim, are randomly distributed on the relatively smooth and even surface. Branchial openings are evenly spaced, and the rims of the stellate apertures are lined with spicules. The upper layer of test over the common cloacal cavity and the basal layer, beneath the cavity are of more or less equal thickness. The upper layer accommodates the long branchial siphons and the lower layer the abdomina. The common cloacal cavity is an extensive horizontal space interrupted by thoraces of the zooids which are associated with a thin strip of test along their ventral surface. Spicules are not as crowded in this strip of test as they are in the remainder of the test.

Spicules are stellate, occasionally to 0.072mm diameter, with 13–15 very pointed conical rays in optical transverse section. The rays are actually quite short, being supported on a large central spherical mass and the ray length/spicule diameter ratio is up to 0.25.

ZOOIDS. Zooids have a large branchial siphon to accommodate the thick surface layer of spicule-filled test. Six points are around the rim of the aperture. The atrial aperture is wide exposing a

large part of the branchial sac directly to the cloacal cavity. A conspicuous, usually deeply divided bifid atrial lip projects from the anterior rim of the opening and is inserted into the test above the common cloacal cavity. A large circular lateral organ is on each side of the thorax at the level of the second row of stigmata. A long narrow retractor muscle is free from about half-way down the long oesophageal neck and projects vertically toward the base of the colony. The branchial sac has about 8 stigmata in the anterior row, although these could not be accurately counted in other rows. The gut loop lies horizontally in the basal layer of test and its ascending limb curves up over the gonads. Seven male follicles constitute the testis, and the vas deferens coils 3 times around it, the last coil passing either inside or outside the ovary. Larvae are not known.

REMARKS. The conspicuous characters of this species, apart from the extensive hard sheet-like colony of very even thickness, are its numerous pointed spicule rays, and long branchial siphon and oesophageal neck. Other characters such as the conspicuous atrial tongue, retractor muscle, few coils of the vas deferens, numerous larval epidermal ampullae and a larval blastozooid, are in many *Polysyncraton* spp. *P. meandratum* has fewer vas deferens coils, fewer male follicles, a different colony, spicules present only in a surface layer, and globular or burr-like spicules with rod-shaped rather than conical rays. The species does not appear to have spicules as diverse or as large as in *P. scobinum* which has blunt-tipped spicule rays as well as conical ones and spicules to 0.14mm diameter, with fewer and not such sharply pointed rays, present mainly in a layer at the surface and within a layer on the base. *P. millepore* Vasseur, 1969 an Indo-West Pacific species, resembles the present species in many aspects of its colony, zooids and larvae. It has smaller spicules with fewer rays, a very narrow atrial lip (which sometimes is forked at the tip but never is bifid like the present species), 5 (rather than 3) coils of the vas deferens, and only 2 or 3 testis follicles.

The species has some similarities to *P. pseudorugosum* which has been recorded a number of times from the Arafura Sea. However, its surface sculpture, its common cloacal systems, shorter branchial siphons, and fewer less pointed spicule rays establish it as a different species.

Records of the present species indicate that it could be expected to have a wider range in the tropical Indo-West Pacific.

Polysyncraton circulum Kott, 1962
(Figs 42B–E, 161G, H)

Polysyncraton circulum Kott, 1962: 298; 1998: 89.

NEW RECORDS. Queensland (Wistari Reef, QM G308131; Heron Island, QM G302143, G302501, G302973, G308191, G308246, G308249-51, G308253, G308440; Swain Reefs, QM G308407).

PREVIOUSLY RECORDED. Queensland (Moreton Bay, Mackay – Kott, 1962).

COLONY. Colonies are fleshy investing sheets, with small spicules crowded in the surface test, making it white and hard, often raspy to the touch, and quite wrinkled or loose-looking in preservative. Sometimes minute, spicule-filled papillae are crowded at the surface of the colony (see QM G308407). Spicules are present also in the base, but are sparse in the remainder of the colony. Often spicules line the margins of the stellate branchial apertures, or a plug of spicules is in the siphon in contracted specimens. Branchial apertures sometimes are minute, without spicules around them. The surface spicules are interrupted by large, transparent spherical vesicles about 0.05mm in diameter, about 0.1–0.2mm apart, and arranged in a circle around each branchial aperture. Common cloacal cavities are thoracic, with large and irregular apertures with frilled lips often elevated above the surface. Some colonies (QM G302143) have circular grooves in the surface where it is depressed over deeper primary common cloacal canals that surround clumps of zooids.

Most living colonies are orange-chrome[R], coral red[R] colour or bright flame scarlet[R] with orange or scarlet vesicles around the branchial apertures, but one (QM G308251) is cinnamon rufus[R]. Zooids are orange too. In preservative the colonies are white, the vesicles transparent and colourless, eggs and embryos are yellow to orange, but generally zooids are transparent.

Spicules are globular or burr-like, most with crowded, long rod-like, flat-tipped, cylindrical rays, but others have flattened rays with pointed tips and a few have widely separated short conical pointed tips projecting from the surface of the spherical central mass of the spicule or from polygonal bases. Spicules are variable in size, to 0.065mm in diameter. Some appear to be hollow in the centre.

Prochloron is often present in patches on the

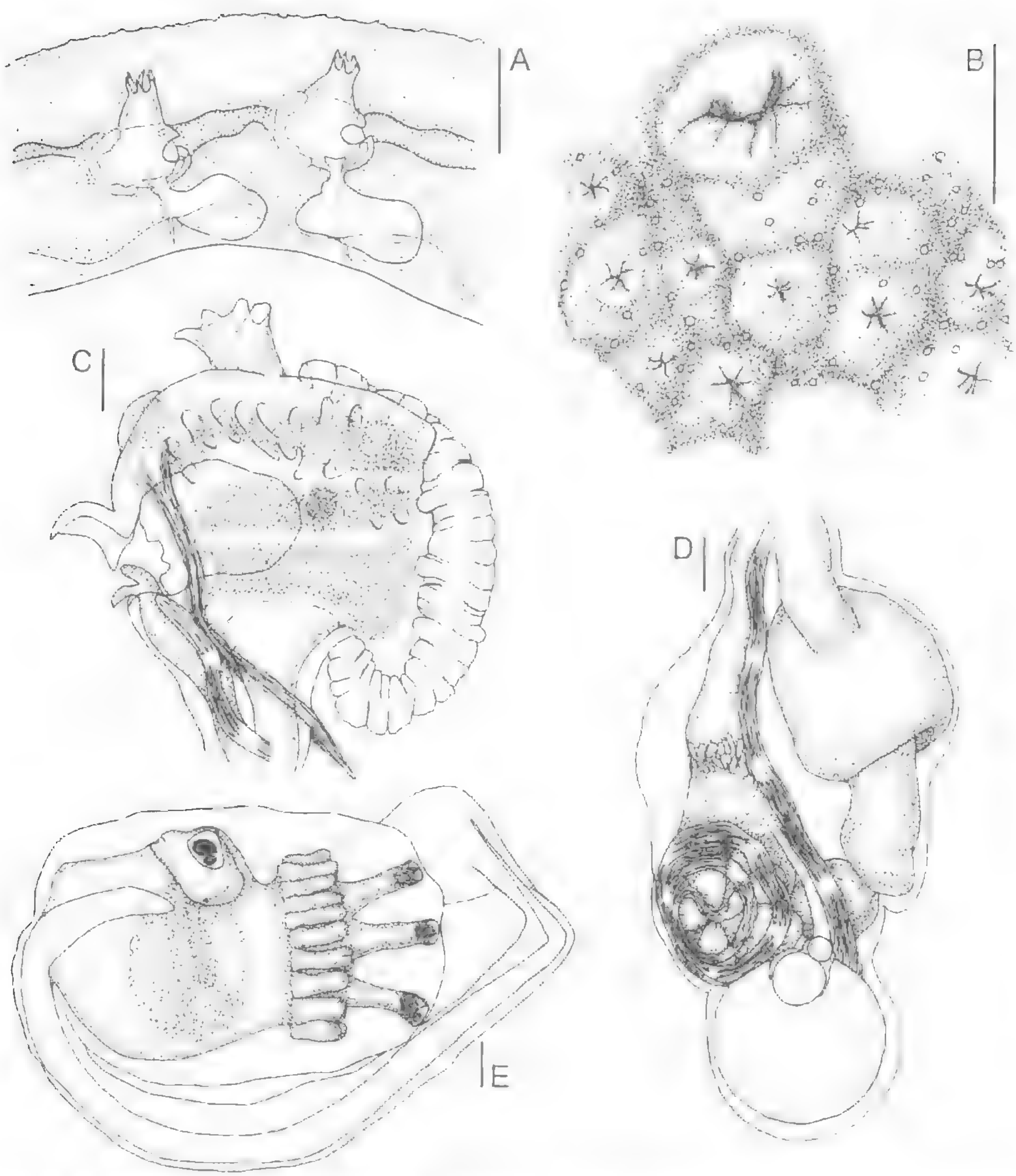


FIG. 42. A, *Polysyncraton arafurensis* (WAM 108.93) – A, semidiagrammatic vertical section through colony. B-E, *Polysyncraton circulum* (B, QM G308249; C,D, QM G308246; E, QM G308191) – B, part of colony surface showing a common cloacal aperture, branchial apertures, and circle of vesicle cells around each branchial aperture; C, thorax; D, abdomen; E, larva with adult organs (gut and branchial sac) not well advanced. Scales: A, 0.5mm; B, 1.0mm; C–E, 0.1mm.

surface of the colony. Part of one colony has zooids at the surface in raised blisters of the test (QM G302143).

ZOOIDS. Zooids are small, to about 1.0mm long overall but robust. The 6 branchial lobes are rounded. A large muscular atrial tongue is on the upper rim of the opening. The short retractor muscle projects from the postero-ventral part of the thorax. Two large stolonic vessels project from the ventral side of the gut loop. About 10

stigmata are in each row in the branchial sac. The gut loop is open, with the proximal end of the ascending limb curved up over the gonads. The testis has up to 6 follicles in a crowded circle surrounded by 3 coils of the vas deferens. The outer coil of the vas deferens passes around the outside of the developing egg which separates it from the other coils. Embryos are being incubated in the basal test of colonies collected in September from Heron I. (QM G308191, G308246). Larvae are large, the trunk 1mm long, with the tail wound about three quarters of the way around it. There are 8 lateral ampullae on each side of the 3 antero-median adhesive organs. The adhesive organs themselves are small, supported on the ends of long, stout stalks. A large external lateral ampulla projects vertically from the waist of the left side of the trunk.

REMARKS. The spicule rays sometimes resemble those of *Didemnum arancium*, with short conical tips projecting from the surface of otherwise globular spicules. However, its generic characters distinguish it. *P. poro* Monniot & Monniot, 1987, has the same type of spicules in the same size range but is distinguished from the present species by their distribution throughout the test rather than being confined to 2 layers as they are in the present species. *P. meandratum* also has similar spicules but they are in a discontinuous layer beneath a conspicuous superficial layer of bladder cells. The vesicles in the surface test surrounding the branchial apertures resemble *P. orbiculum* Kott, 1962, although in that species the spicules are throughout the test and are distinctly stellate with fewer rays than the present one.

Some aspects of this species, including the spicules and their distribution and the gonads (including the vas deferens) resemble *P. pulchrum* although the zooids of the latter species are larger, the cloacal cavity more extensive (being posterior abdominal rather than thoracic, as it is in the present species) and the large vesicles interrupting the spicules in the surface test are not present. Also the common cloacal apertures in the latter species are terminal and the colonies are upright, while in *P. circulum* the common cloacal apertures are sessile and randomly distributed with the atrial lips of adjacent zooid always associated with the opening. In *P. pulchrum* atrial openings are sessile without an atrial lip, and open directly into the posterior abdominal cloacal cavity.

Kott (1962) described larvae from the type material as having only 6 lateral ampullae. Re-examination of this material has shown that some of the ampullae are in the process of subdivision. The larvae are the same size, with the same long stout stalks of the adhesive organs as the present ones. Blastozooids were not observed.

Polysyncraton dentatum sp. nov.
(Figs 43, 162D; Pl. 4G)

TYPE LOCALITY. Western Australia (east of Cape Naturaliste, western end of Bunker Bay, 4 to 5m on rocks, coll. K.L. Gowlett Holmes 22.1.93, holotype SAM E2677).

COLONY. The holotype colony is an irregular plate, about 3cm diameter. Large, evenly spaced common cloacal apertures are on the upper surface. Radially arranged ribs of spicule-filled test in the roof of the common cloacal cavity, just inside the common cloacal apertures, are visible through the spicule-free test surrounding the rim of each aperture and convey a toothed appearance to the aperture. Generally, spicules are mixed with bladder cells and dark pigment in the superficial layer of test, but lines of pigment in the surface where spicules are absent or sparse create an overall net-like pattern with a branchial aperture in the centre of each polygonal mesh of the net. Spicules become relatively crowded at thorax level, but are reduced in number toward the base, at abdomen level, where they are quite sparse. A plug of minute spicules are in each moderately long branchial siphon where the zooids are particularly contracted and withdrawn down into the soft test. However, sometimes the spicules appear to outline stellate apertures.

Spicules are relatively small, to 0.04mm diameter. Many are globular with thick, compact, flat-tipped cylindrical rays, but others have 20–22 short conical rays in optical transverse section. The common cloacal cavity is shallow and thoracic.

ZOOIDS. Zooids are darkly pigmented, robust and muscular, but they are contracted in the only available colony. In these contracted specimens, the outer body wall and siphons are covered with projecting spatulate columnar cells, about 0.007mm long and about 0.004mm wide. The branchial siphon is robust and muscular with the rim divided into 6 pointed lobes. A long atrial tongue, bidentate at the tip, projects from the upper rim of the aperture. Lateral organs on each side of the thorax are large and everted. A short and strongly tapered retractor muscle projects

from the upper part of the oesophageal neck. Although 4 rows of stigmata were detected in the branchial sac, it was not possible to count the numbers per row. The gut is voluminous, with a long duodenum and a short, wide almost trumpet-shaped posterior stomach which meets the wide proximal end of the rectum in the pole of the gut loop. The rectum has a posteriorly projecting elbow just beyond its junction with the posterior stomach. The diameter of the rectum steadily reduces anteriorly toward the atrial aperture. Gonads were not detected in these zooids.

REMARKS. Despite the absence of gonads, the specimen is assigned to *Polysyncraton* on the basis of its robust zooids with muscular thorax, large bidentate atrial lip and short posterior stomach increasing in diameter to its junction with the rectum (rather than being separated from it by a distal constriction).

The spatulate projecting epithelial cells on the surface of the thoracic body wall are known in other species of Didemnidae (see glossary, **epidermis**). Although they undoubtedly are brought closer together with contraction of the zooids, they do not appear to result from contraction or elasticity in the body wall and epidermis.

Didemnum chartaceum has a similar mixture of globular and stellate spicules as the present species but they are larger and crowded in a single layer, and (in addition to its generic characters) its darkly pigmented test crowded with bladder cells distinguishes it. Tropical *Didemnum oblitum* has similar but larger globular spicules but it lacks the stellate ones of the present species. Tropical *P. dromide* has similar small burr-like and globular spicules with flat-tipped and pointed rays but generally the rays are longer and less compact than in the present species, the colonies differ (*P. dromide* having zooids along each side of circular canals that surround stands of solid test), and the retractor muscle is particularly short. The tropical *P. rugosum* has burr-like spicules with separated and sometimes chisel-shaped rays rather than the flat-tipped rays forming the globular spicules of the present species. Spicules are most like those of *P. meandratum*, but its fleshy colonies, with spicules confined to a single layer beneath the superficial layer of test, distinguish it from the present one. *P. flammeum* from eastern Australia also has similar spicules, but none with regularly pointed conical rays, and its spicules are largely

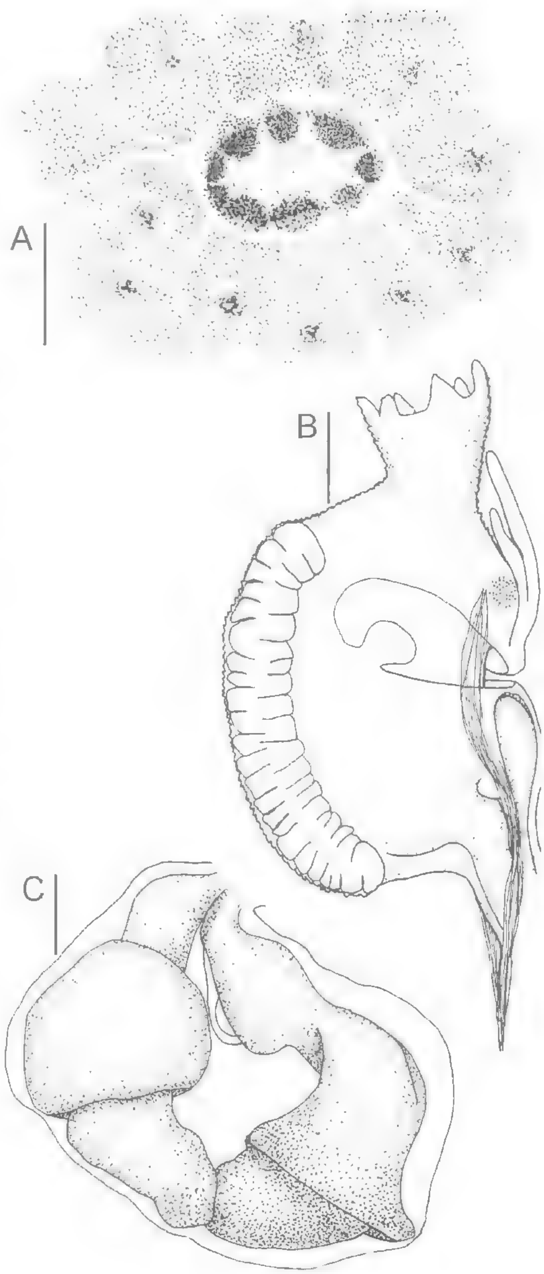


FIG. 43. *Polysyncraton dentatum* sp. nov. (SAM E2677) – A, colony from upper surface showing spicules forming radial thickenings around rim of common cloacal aperture; B, thorax showing atrial aperture with lateral organ on the edge and atrial tongue folded back against zooid; C, gut loop, ventral view showing conspicuous elbow on expanded proximal part of the rectum, and the ovary just visible from dorsal side of the distal part of the rectum. Scales: A, 1.0mm; B,C, 0.1mm.

confined to a single layer that looks like a veil over the surface of the colony.

The radial ribs in the roof of the cloacal cavity around the common cloacal aperture occur in other species. They are visible from the surface because spicules, though present in the ribs are absent from the surface test in that area.

Polysyncraton discoides Kott, 1962
(Figs 44, 161F; Pl. 4H)

Polysyncraton discoides Kott, 1962: 303 (part, syntypes from Rottnest I.); 1998: 89.

NEW RECORDS. Tasmania (Port Davey, SAM E2623).

PREVIOUSLY RECORDED. Western Australia (Rottnest I. – syntypes AM Y1482 Kott, 1962).

COLONY. Syntype colonies are small circular cushions about 1cm in diameter and 1.5mm thick with a single central common cloacal aperture. The specimen from Port Davey is a more extensive sheet with large, randomly distributed, closed common cloacal apertures with thin frilled margins. The surface is smooth, although sometimes crinkled (like crushed paper) in preservative. All colonies have spicules crowded in the surface test. Elsewhere they are slightly less crowded, but never sparse. On the surface they line the branchial siphons and the 6-lobed stellate apertures are clearly outlined by spicules. Generally they are to 0.03mm in diameter, and more or less globular or burr-like. Rays are numerous, long and straight with irregular to flat and sometimes rounded but seldom pointed tips. The common cloacal cavity is thoracic, except around clumps of 5–10 zooids where it extends the full length of the zooid. In preservative all colonies are white.

ZOOIDS. Zooids of the syntypes are small, contracted and not in good condition; although re-examined their structure was not resolved. Gonads were not detected. Zooids from the Tasmanian specimen are robust to nearly 2mm long. They have a distinct but not especially long, cylindrical to funnel shaped branchial siphon with 6 pointed lobes around the rim. A broad muscular atrial lip often with a spreading concave tip projects from the upper rim of the large, sessile atrial opening. A large (0.1mm diameter) lateral organ is present. About 8–10 stigmata per row are in the branchial sac. Although strong dorsal pharyngeal muscles are present, a retractor muscle projecting from the posterior end of the thorax was not detected. The gut forms a simple vertical loop, and is divided into the usual parts. Most zooids of the Tasmanian material have a large egg in the abdomen, and only one zooid was detected with 6 male follicles surrounded by 3 coils of the vas deferens.

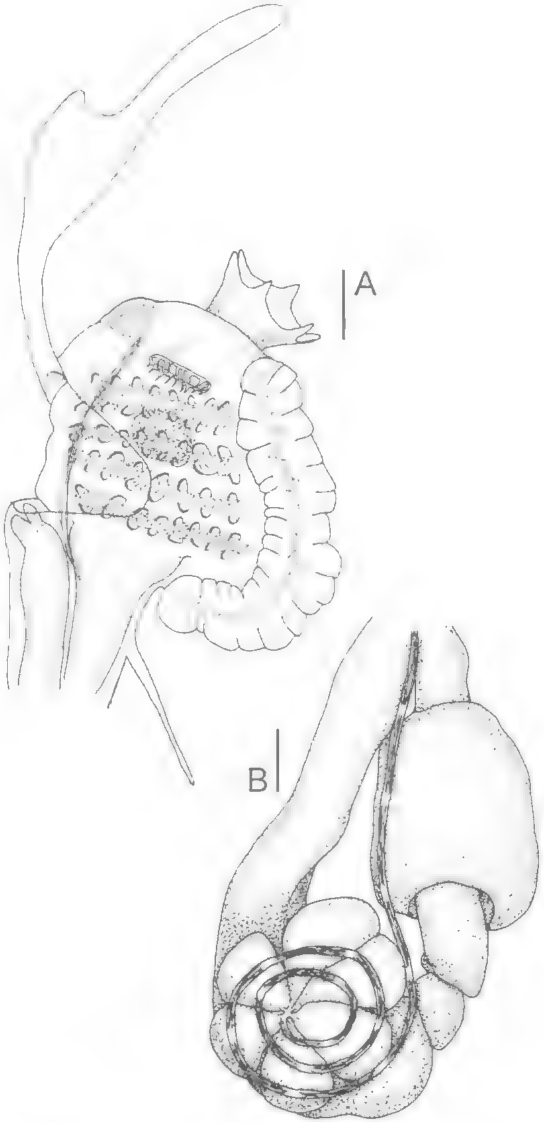


FIG. 44. *Polysyncraton discoides* (SAM E2623) – A, thorax; B, gut loop and testis. Scales: 0.1mm.

REMARKS. Kott (1962) invoked the zooids of the Tasmanian *P. paradoxum*: Kott, 1954 (which she believed were conspecific) in her description of *P. discoides*. Although, *P. discoides* syntypes have similarly shaped colonies and spicule distribution (the spicules being particularly crowded in the hard surface and basal layers of test) to *P. paradoxum*: Kott, 1954 (< *P. papyrus*), the latter has stellate rather than globular or

burr-shaped spicules. The Western Australian *P. orbiculum* also is distinguished by its stellate spicules.

P. rugosum has similar spicules and zooids and only its pigmented surface test and tropical range distinguish it from the present species. *P. flammeum* has similar but larger spicules confined to a single superficial layer and smaller zooids. There appears not to be any atrial lip and only 2 coils of the vas deferens were detected.

Records of this species are few, and from a wide geographic range. Nevertheless the colonies, zooids and spicules are identical and distinguishing characters were not detected. It is probable that the species is a temperate one, with a range across the southern coast of the continent.

Polysyncraton dromide sp. nov.
(Figs 45, 162E)

TYPE LOCALITY. Northern Australia (Torres Strait, Robert I. 9°59'S 143°07'E, 16-30m, coll. Queensland Fisheries Service, Northern Fisheries Survey, FV Jennifer Ruth, from back of a dromid crab, grid 9931 02.02.72, holotype QM G301568).

FURTHER RECORDS. Western Australia (Cockburn Sound, WAM 191.91).

COLONY. The holotype colony is an inverted saucer, the lower concave surface fitting onto the crab carapace. The upper (convex) surface is broken up into raised zooid-free shallow domes (to 5mm diameter) by depressions in the surface test over the circular cloacal canals. Zooids are embedded in the test along each side of these canals, the atrial apertures opening directly into them. The course of the cloacal canal is emphasised by the thick layer of crowded spicules along the top of the canals, and yellowish-white opaque pigment over the spicules. The colony from Cockburn Sound is an extensive, robust but gelatinous slab, less regular than the holotype and with spicules sparsely and unevenly distributed in the surface. In this specimen the deep primary common cloacal canals surround clumps of zooids rather than zooid-free areas of test. In both recorded colonies the circular canals are deep, extending the whole length of the zooids, and sometimes deeper than that. They extend horizontally between the thoraces in the clumps of zooids. Spicules extend from the layer in the surface test over the common cloacal canals to form a thin layer lining the canals. Spicules are not present elsewhere in the colony.

Spicules are up to 0.04mm in diameter and are burr-like, with about 15–17 long flat-, round-tipped or pointed rays in optical transverse section. They disintegrate readily.

In preserved specimens the test in the basal half of the colony and in the zooid-free parts between the canals is transparent in section but slightly grey-blue when viewed from above.

ZOOIDS. Zooids are moderately large, about 2mm long of which the wide thorax and distal part of the abdomen (from the base of the oesophagus) are each about one-third, while the oesophageal neck and branchial siphon are each about one-sixth of the total length. The long branchial siphon reaches through the thick spicule layer over the cloacal canal. Six small branchial lobes line the rim of the aperture. A flat bifid lip projects from the anterior rim of the atrial aperture which is sessile exposing most of the branchial sac directly to the cloacal cavity. The branchial sac has 4 rows, each of 12 to14 stigmata. The gut forms a long, vertical loop. It is divided into a relatively long and narrow stomach, a long, wide duodenum and the mid gut which expands to join the rectum in the pole of the gut loop. The diameter of the rectum is much reduced in its upper (distal) part. The testis is divided into about 20 follicles clustered together on the dorsal side of the posterior end of the gut loop. The vas deferens is in 3 wide spirals around the top of the clump of testis follicles.

A few embryos are present in the basal test of the holotype, some as tailed larvae. Larvae are large, the trunk 1.5mm long with the tail wound only halfway around it. Twelve pairs of finger-like ectodermal ampullae are around the anterior end of the trunk at the base of the median adhesive organs, a large external lateral papilla projects horizontally from the left side of the waist of the mature larva, an oozooid and 2 blastozooids (one on each side) project out into the larval test and 4 rows of stigmata are on each side of the pharynx of both oozooid and blastozooid.

REMARKS. Most characters except the cloacal systems are similar in both the specimens assigned to this species. The difference in the cloacal systems may occur when vegetative zooids form clumps in otherwise zooid-free areas.

Both *P. nigropunctatum* Sluiter, 1909 and *P. magnetae* Hastings, 1931 have similar colonial systems to the holotype. Like the present species, spicules of *P. nigropunctatum* are restricted to the surface test, especially along the top of, and lining the cloacal canals and in the base of the

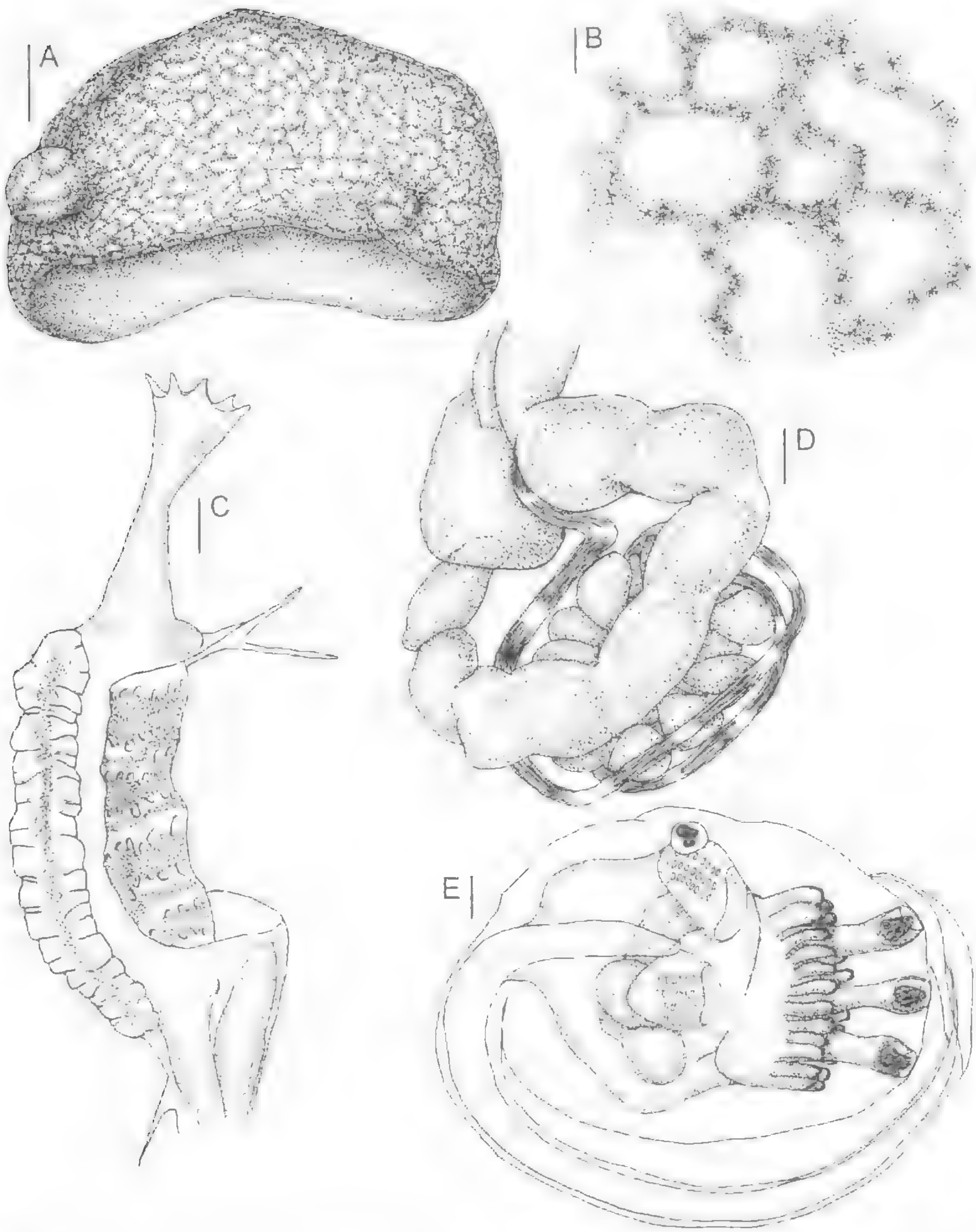


FIG. 45. *Polysyncraton dromide* sp. nov. (QM G301568) – A, colony; B, part of surface showing zooid openings along canals surrounding solid zooid-free stands of test that protrude from the surface of the preserved colony; C, thorax; D, ventral view of abdomen; E, larva. Scales: A, 1.0cm; B, 2.0mm; C–E, 0.1mm.

colony, although they form continuous rather than uneven layers in the surface and base of the colony. In *P. magnetae* they are present throughout. *P. nigropunctatum* has conspicuous black pigment bodies not observed in the present species, and it lacks the small burr-like spicules. Certain species in other genera have similar cloacal systems and the preserved specimens are

similar in appearance, with elevated zooid-free areas or clumps of zooids surrounded by depressed areas over the common cloacal canals. Usually these zooid-free areas contain spicules, unlike the present species which has clear, glassy aspicular test in these areas. The long branchial siphons and numerous testis follicles are also conspicuous characteristics.

P. meandratum has similar colonies, although the branching canals do not always join up into such conspicuous circles, and its spicules are larger with more rays.

The larva is larger than usual for this genus, although 12 ectodermal ampullae on each side is unusual, 8 being the more usual number. The larva resembles *P. magnilarvum* Millar, 1962 from South Africa which also has a large larval trunk, about 15 pairs of epidermal ampullae and a larval blastozooid. The present species is distinguished by its small burr-like spicules, the South African species having stellate spicules to 0.075mm in diameter.

Polysyncraton echinatum sp. nov.
(Figs 46, 163F; Pl. 5A-C)

TYPE LOCALITY. Queensland (Wistari Reef, near landing stage, low tide, coll. P. Kott et al. 15.03.93, holotype QM G302987; Heron I., eastern end of reef, coll. P. Kott et al., 19.03.93, paratype QM G300911)

FURTHER RECORDS. Queensland (Capricorn Group, QM G300907, G301897, G308001; Big Broadhurst Reef, QM GH5349; Whitsunday Is, QM GH5370; Bowden Reef, QM G300993; Hinchinbrook I., QM GH282; Lizard I., QM G304176).

COLONY. Colonies are gelatinous, thin, encrusting sheets to more robust irregular shapes with the surface raised into long ridges with common cloacal apertures along the top or rounded swellings to finger-like lobes with terminal cloacal apertures. One long colony (QM GH5349) has the upper surface highly arched, while the flat base is attached to the substrate. Another (QM G300911) is a fleshy upright lobe, laterally compressed. The surface swellings and ridges result from thickenings of the basal layer of test, that raise the height of the colony beneath the terminal common cloacal aperture. The common cloacal cavities are 3-dimensional, primary circular canals being the full depth of the zooids but often becoming posterior to clumps of zooids, and penetrating them at thorax level leaving the thoraces surrounded by the common cloacal cavity. Clumps of abdomina are embedded in common test, each clump attached to the thick firm basal or central test by a narrow connective. The common cloacal cavity expands into a larger chamber beneath each terminal cloacal aperture. The most conspicuous features of many colonies are the pointed papillae each usually associated with a branchial aperture and directed toward the common cloacal aperture. The most ventral branchial lobe of the 6 surrounding the aperture is particularly long and is inserted into the pointed papilla. Other slight surface protrusions are associated with the other 5 branchial lobes. In one colony (QM G304176) these pointed papillae are particularly large (nearly 1mm long) and conspicuous, directed up toward the common cloacal apertures, with the branchial apertures on their upper surface (i.e. the side against the colony and facing the common cloacal aperture). In this colony, which has protuberant lobes with terminal cloacal apertures, 10 to 12 pointed papillae directly surround the cloacal apertures. However, papillae are not always present (QM G300911, G308001).

A band of spicule-free test is around the frilled rim of each large, circular, common cloacal aperture. Sometimes spicules crowd the branchial siphon lining forming a margin of white spicules around the stellate apertures but in one colony (QM G300993), they are in 3 short double rows projecting into the siphon lining. A single, continuous layer of crowded spicules is at the surface, which is raspy to the touch. This layer of spicules is continuous with those in the surface papillae. Spicules are also in a layer on the base of the colony but are only sparse in the remainder of the test. Spicules are to 0.055mm diameter. They are conspicuously stellate with long, conical and pointed rays, 7–11 in optical transverse section. The ray length/spicule diameter ratio is about 0.4.

Living colonies sometimes are a van dyke brown[R] colour with seal brown[R] pigment cells (QM G302987); or heliotrope purple[R] and brown (G308001); or maroon-purple[R] (QM G300911); or bright orange (scarlet[R]) with scarlet[R] or vermilion[R] zooids (QM G300907) in the surface of the colony. In preservative the zooids are cream and the label stains brownish yellow.

ZOOIDS. Zooids are relatively large, about 1.8mm long when relaxed. Branchial lobes are usually narrow, relatively long and pointed and the ventral one (extending up into the large surface papilla) is particularly long and narrow. A long, narrow, bifid atrial tongue sometimes stretches out from the upper rim of the very large atrial opening, or is contracted to form a transverse flap. Large, oval, lateral organs on each side of the thorax are conspicuous because

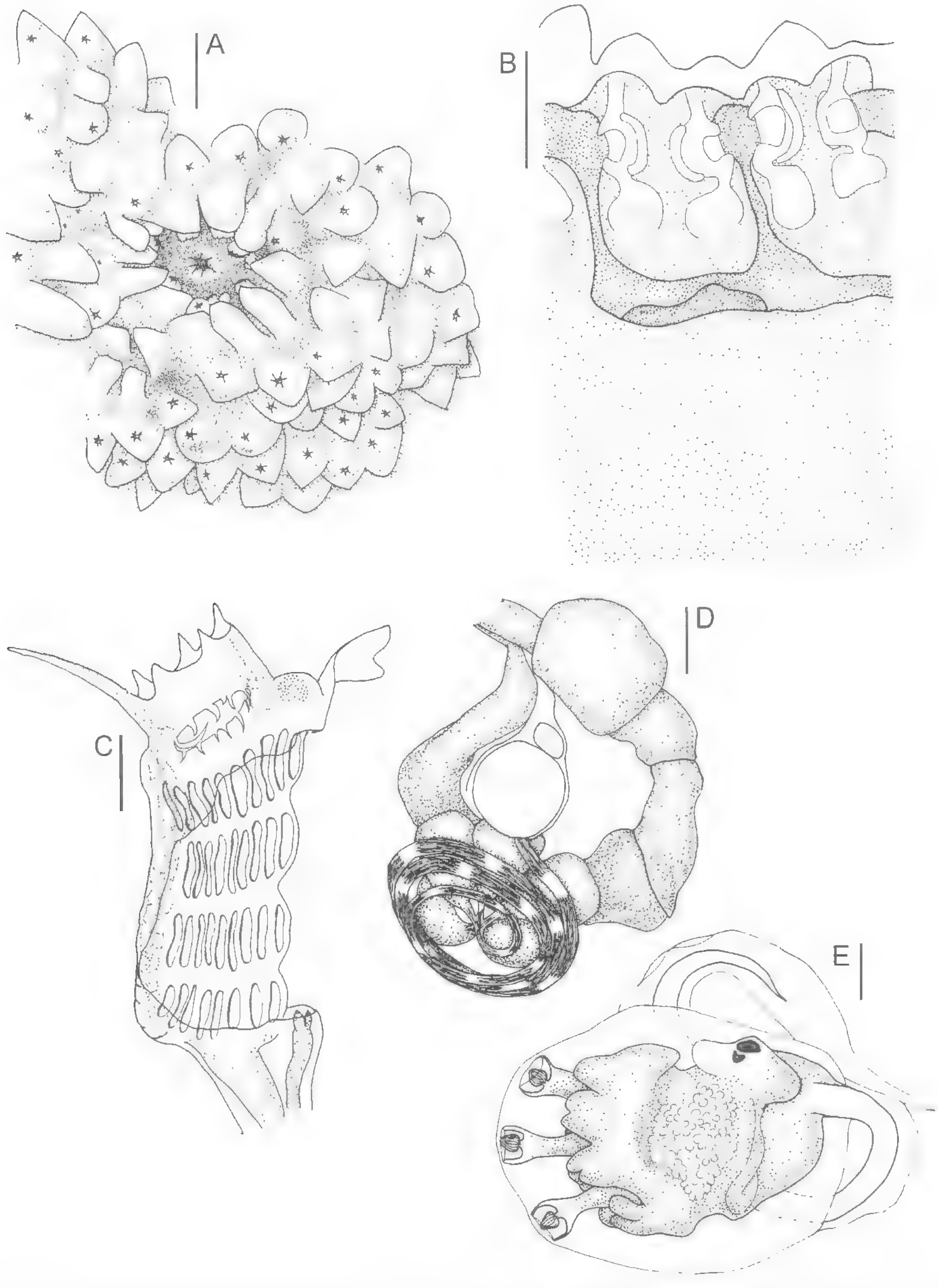


FIG. 46. *Polysyncraton echinatum* sp. nov. (A, QM G304176; B,E, QM G300993; C, QM GH5349; D, QM G302987) – A, top of colony lobe, showing terminal common cloacal aperture surrounded by branchial apertures, each with a pointed ventral papilla; B, semidiagrammatic vertical section through colony (primary cloacal cavities darkly shaded); C, thorax showing long ventral branchial lobe and atrial tongue; D, abdomen; E, larva. Scales: A, 2.0mm; B, 1.0mm; C–E, 0.1mm.

few other spicules are in the test around the zooids. A retractor muscle was not detected. The thoracic musculature is not conspicuous, and both holotype and paratypes have a large extended thorax. About 10 long, narrow stigmata are in the anterior row, and these reduce to 8 in the last row. The gut loop is wide with the ascending limb looped up over the gonads. Five or 6 testis follicles are in a circle with 4 coils of the vas deferens around its outer circumference. A single larva in a colony from Lizard I. collected in April is not well advanced, but well developed larvae are in the specimen from Bowden Reef, also collected in April. The tail is wound about three quarters of the way around the yolky trunk, which is 0.6mm long, has 3 antero-median adhesive organs, an otolith and an ocellus, and 4 subdividing ectodermal ampullae on each side.

REMARKS. The large atrial opening exposes the whole of the perforated pharynx (as in *Diplosoma* and *Lissoclinum* spp.), the large extended thorax with weak muscles and the stellate spicules with relatively few rays are unique features of this species. The rather fleshy colonies with the spicules confined to the thin surface and basal layers are also useful features contributing to its characterisation. Although colonies of *P. meandratum* and *P. purou* are similar, the species is readily distinguished by its stellate spicules with relatively few conical rays. A similar large atrial aperture is known for *P. poro* Monniot & Monniot, 1987, which is distinguished from the present species by its fewer vas deferens coils, and its spicules (with more numerous and shorter rays). Spicules have fewer and less sharply pointed rays than those of *P. arafurensis* which they otherwise resemble. Pointed surface papillae, like those in *Didemnum cuculliferum*, are not always present, and are not a reliable character for identification.

In some of these colonies (see especially QM G304176) orientation of the dorsal surface of each zooid (especially in those zooids immediately surrounding the common cloacal apertures) toward a common cloacal aperture is emphasised by the large ventral branchial lobe and its associated papilla. The branchial aperture opens on the side of the papilla facing the common cloacal aperture (i.e. the under surface of the papilla, as it is inclined up against the colony, its point toward the cloacal aperture in these preserved colonies). The incurrent stream of water is therefore drawn down from around the top and sides of the colony, while the excurrent stream goes out through the centre of this area. This arrangement differs from that found in colonial species, where incurrent apertures usually face the opposite direction from the excurrent ones (Kott, 1989). The dynamics of incurrent and excurrent water around the common cloacal aperture in this, and possibly other didemnid species is not understood.

Polysyncraton flammeum sp. nov.
(Figs 47, 161E; Pl. 5D)

TYPE LOCALITY. Queensland (Kings Beach Caloundra, low tide under rubble, coll. P. Kott, 1.8.97, syntypes QM G308461, 2 specimens).

COLONY. The syntype colonies are small (to about 3cm greatest dimension) thin, oval cushions with rounded margins and a thin surface layer of spicules that, in life, forms a whitish pink veil over the orange test. Zooids are orange and the branchial apertures opening on the surface (on slight prominences) are orange. In the surface layer, spicules are interrupted by orange vesicles (about 8) in a circle around each branchial aperture. The preserved colonies are white and flattened and the zooids are white. The cloacal cavity is thoracic.

Spicules are very sparse in the test beneath the surface layer. They are relatively small to 0.05mm diameter, with flat or irregularly tipped rays. Regular conical points are not present.

ZOOIDS. Zooids are about 1.5mm long. A retractor muscle is not present. The branchial siphon is a short, wide cylinder with 6 points around the rim. The atrial aperture is a wide, sessile opening exposing much of the branchial sac directly to the common cloacal cavity. There does not appear to be an atrial lip. The branchial sac is large and rectangular with 12 long stigmata in the anterior row, reducing to about 8 in the posterior row. The gut forms a simple circular loop and a circle of 7–9 testis follicles with 3 coils of the vas deferens is against its dorsal side. Larvae are not known.

REMARKS. The species resembles *P. discoides* in its 3 coils of the vas deferens and almost globular spicules, although they are larger (*P. discoides* having spicules to 0.03mm diameter). The latter species has larger zooids (to 2.0mm overall), a long atrial tongue sometimes divided at the tip and spicules throughout the colony. *P. sagamiana* Tokioka, 1953, from Sagami Bay and apparently conspecific material from Palau Is (Tokioka, 1967) have similar spicules and zooids to the present species, but are distinguished by an

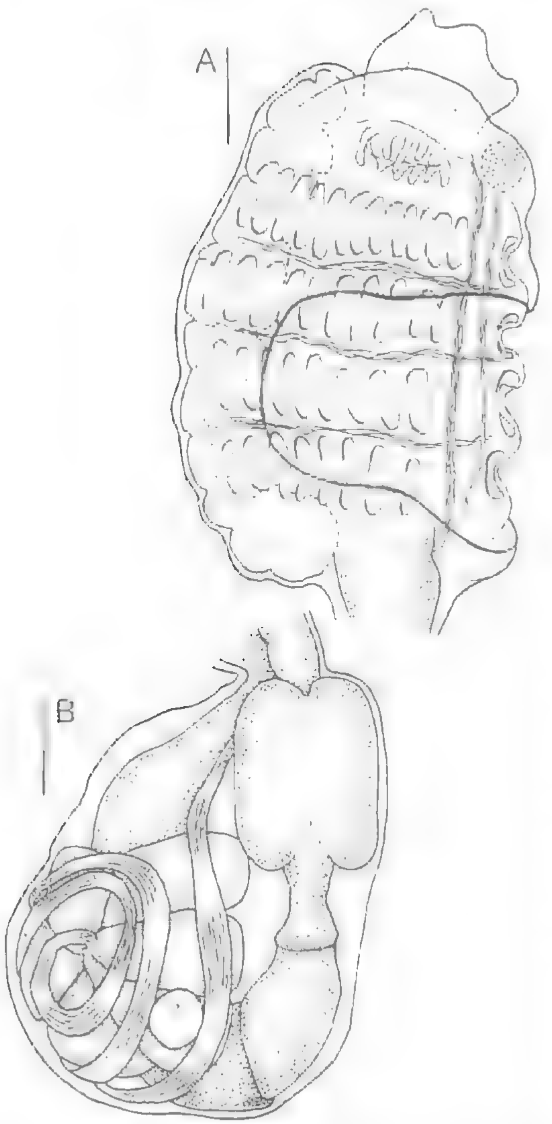


FIG. 47. *Polysyncraton flammeum* sp. nov. (QM G308461) – A, thorax; B, abdomen. Scales: 0.1mm.

atrial tongue (like *P. discoides*) and spicules crowded throughout. *P. circulum* has similar vesicles in circles interrupting a superficial layer of spicules, although its spicules are larger with more regularly conical points than the present species. Spicules are similar in the Western Australian *P. dentatum*, although it has some spicules with short conical rays. It also has some crowded spicules at thorax level that are not in the present species.

Polysyncraton glaucum sp. nov.
(Figs 48, 163G; Pl. 5E)

TYPE LOCALITY. Queensland (Swain Reefs, Frigate Cay, 20m, coll. S. List 27.9.95, holotype QM G305628, paratype QM G305589; Wistari Reef, landing stage, low tide rubble fauna, coll. P. Kott 6.3.93, paratype QM G308057).

FURTHER RECORDS. Queensland (Deloraine I., QM GH5372).

COLONY. Colonies are thin and hard, with the surface marked off into polygonal areas (about 1cm in diameter) by spicule-filled ridges. Each polygonal area has a central common cloacal aperture. These are about 5mm distant from one another, and their rim is divided into 5 or more lobes. The colony is green to olive green in life, the pigment being in the surface test amongst the spicules, while the raised ridges around each system are white. In preservative the colony becomes a dirty brownish to beige colour (especially in the rim of the common cloacal apertures, from which spicules are absent) while the basal layer, beneath the horizontal thoracic common cloacal cavity, is white. Zooids are orange in preservative. Branchial apertures are stellate. Each polygonal area is a separate system about 5mm in diameter, the cloacal cavities being isolated from one another. About 50 zooids are in each system. Each thorax crosses the cloacal cavity in a separate test sheath.

Spicules are crowded throughout the test, but sometimes minute blisters or vesicles are embedded amongst them in the surface test and the spicules are most crowded in the base of the colony. They are stellate to 0.09mm in diameter with about 9–11 moderately long tapering conical to almost rod-shaped rays in optical transverse section. Even the conical rays are seldom particularly pointed. Rays are often broken. The ray length/spicule diameter ratio is about 0.33.

ZOOIDS. Zooids are of moderate size, about 1.5mm long. The thorax is robust, with long fusiform stigmata often pointed at each end. There are 10 in the first row, 8 in the next 2 rows and possibly 7 in the last row. The short branchial siphon has 6 sharply pointed lobes around the opening. A well-formed, bifid atrial tongue of variable length projects from the anterior rim of the atrial aperture. The longest atrial lips are from the zooids immediately surrounding the cloacal apertures, and are inserted into the slightly frilled rim of the common cloacal aperture. There is a conspicuous circular lateral organ about halfway down the branchial sac. A relatively short fine

retractor muscle is free from the top of the oesophageal neck. The gut forms a wide curved loop with the ascending limb making a wide arc over the gonads. The narrowing of the gut halfway up the rectum is very conspicuous in these zooids. Three coils of the vas deferens surround a circle of 6 male follicles. Embryos were not present in this material.

REMARKS. The distinctive characters of this species are the relatively large zooids with relatively numerous stigmata and an atrial tongue, together with the distinctive cloacal systems and the large spicules. The green colour of this colony is unusual and does not appear to be the result of symbiotic cells. The spicules of the present species have unusually long rays for *Polysyncraton*, larger than in most other species of the genus. *P. scobinum* has spicules about the same size or larger with more numerous and more pointed rays and *P. arafurensis* also has more pointed and more numerous spicule rays. Spicules of *P. echinatum* are similar but are generally smaller with shorter and more distinctly conical rays. These species lack the distinctive isolated common cloacal systems.

The size of the zooids and presence of the atrial tongue are reminiscent of *Didemnum caesium*, however spicules are absent from most of the test except the surface layer in the latter species, the spicules have more, and more pointed, conical rays, and a superficial layer of bladder cells containing black pigment also helps to distinguish it from the present species. *Didemnum scopi* has similar but smaller spicules, and *D. sordidum* has spicules of the same size and form but has dark pigment cells and lacks the unusual isolated systems of the present species.

The discrete cloacal systems distinguish the present species from *Didemnum grande* (which has extensive thoracic, and sometimes deeper, cavities). The rose-coloured colonies of *D. ligulum*: Monniot & Monniot, 1987 from French Polynesia (which the authors refer to as lobulating, or a group of fused colonies) have the same sort of colony as the present species. They also have an atrial lip of various lengths as in the present species. However, the French Polynesian colonies have different spicules, with longer and more numerous sharply pointed rays.

The species, with its thin colony with separated systems and zooids with an atrial tongue, is reminiscent of *P. lithostrotum* which differs in its rounded, almost globular spicule rays and orange

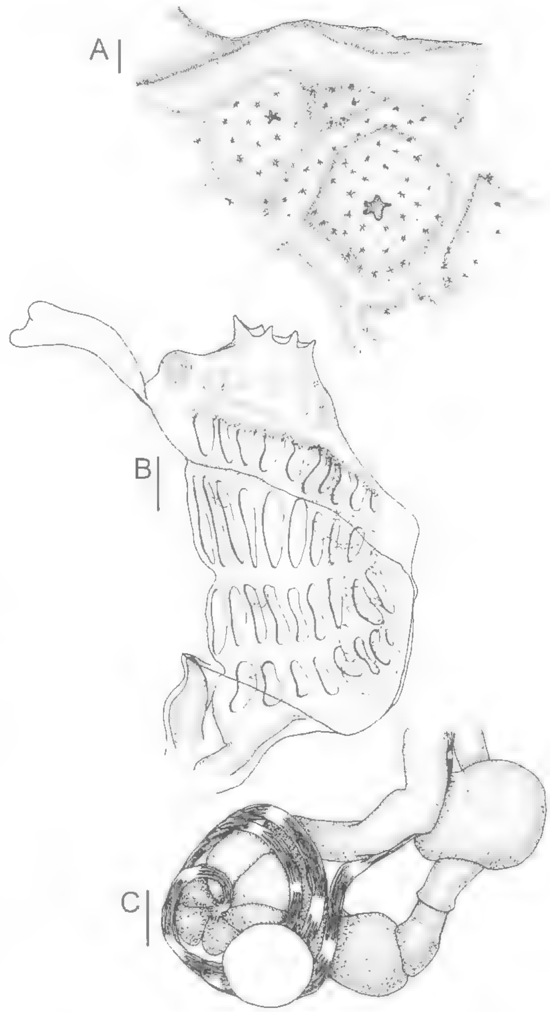


FIG. 48. *Polysyncraton glaucum* sp. nov. (A, QM G308057; B,C, QM G305628) – A, part of upper surface of colony, showing separate cloacal systems with central common cloacal aperture surrounded by branchial apertures; B, thorax; C, gut loop. Scales: A, 1.0mm; B,C, 0.1mm.

colonies. *P. pavimentum* Monniot, 1993 and conspecific *P. lithostrotum*: Monniot, 1993 from New Caledonia also have cloacal systems isolated from one another, but their spicules have pointed conical rays. Both *P. lithostrotum* and *P. pavimentum* are distinguished from the present species by their 2-lobed testis and 6 coils of the vas deferens. *P. multiforme* has similar systems but is a massive red colony with spicules missing from the central test and more numerous spicule rays (to 19 in optical transverse section).

Polysyncraton infundibulum sp. nov.
(Figs 2A,49, 164D)

TYPE LOCALITY. Tasmania (Port Davey, Bathurst Channel, off Jean Point, steep rock slope, 5 to 21m, WEB stan 5, photo PE0367, coll. W. Zeidler, K.L. Gowlett Holmes, F.A. Bavendan 5.4.93, holotype SAM E2610).

COLONY. The large sheet-like colony is flexible, and although spicules are evenly distributed throughout, they are not especially crowded. The branchial apertures are depressed slightly into the surface, and the spicules in the siphonal lining emphasise but do not outline the stellate apertures. The common cloacal cavity is thoracic, each thorax crossing it separately in a ventral spicule-free strip of test. The abdomina are embedded in the basal test, which is relatively thick.

The spicules are variable in size, up to 0.075mm diameter, distinctly stellate with 11-13 short conical rays in optical section. The ray length/spicule diameter ratio is about 0.13-0.2.

ZOOIDS. Zooids have large, funnel-like branchial siphons, each with 6 long narrow lobes around the rim. Relatively large tapering columnar cells projecting from the body wall are crowded on the top of the thorax and the base of the branchial siphon. They are less crowded on the siphon. Atrial apertures are sessile with an anterior lip. Small lateral organs with their opening directed ventrally are on each side of the thorax, about halfway along. A retractor muscle was not detected. The gut is a simple vertical loop. The testis is divided into about 4 follicles with 8 coils of the vas deferens surrounding them.

REMARKS. Distinctive characters of this species are its stellate spicules with relatively short conical rays, its large funnel-shaped branchial apertures with long narrow tentacle-like lobes, and the 8 vas deferens coils (unusually numerous for the genus).

The spicules resemble those of *P. scobinum* but have shorter and less sharply pointed rays and the colonies, though tough, are not as hard. The stellate spicules have a similar number of rays to those of tropical *P. arafurensis*, which has longer and more pointed rays and fewer coils of the vas deferens.

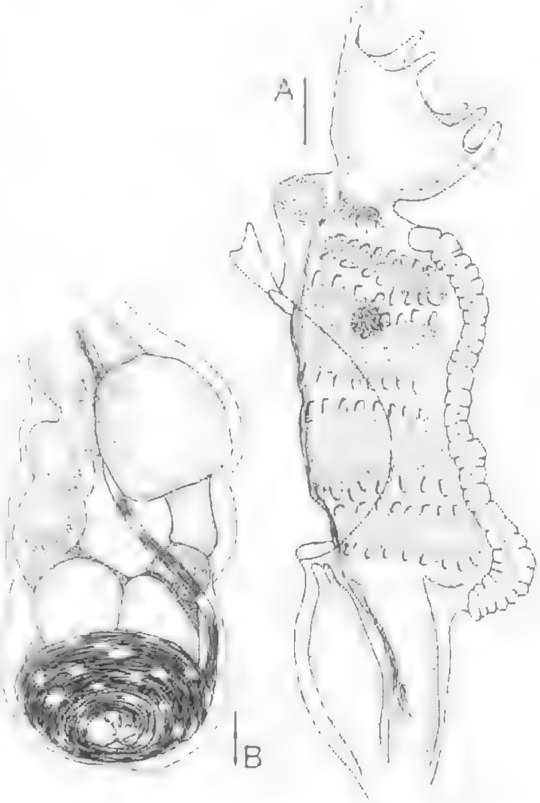


FIG. 49. *Polysyncraton infundibulum* sp. nov. (SAM E2610) - A, thorax; B, abdomen. Scales: 0.1mm.

Polysyncraton jugosum
(Herdman & Riddell, 1913)
(Figs 50, 164F)

Leptoclinum jugosum Herdman & Riddell, 1913: 886 (part).
Polysyncraton jugosum: Kott, 1998: 90.
Polysyncraton chondrilla: Kott, 1962: 296.

PREVIOUSLY RECORDED. New South Wales (Port Jackson, Botany Bay, off Cape Three Points - syntypes AM G12205, G12206, G12209; Newcastle Bight, AM G12207).

COLONY. Colonies are large, upright masses. Sometimes they consist of several rounded lobes (AM G12205), but others are attenuated cones, narrowing to the terminal common cloacal aperture (AM G12206, G12207). The tip of the colony may be subdivided (Herdman & Riddell 1913, pl.92, fig. 1) with a common cloacal aperture on each division. Two specimens (AM G12205 and one from AM G12206) were taken from the backs of crabs and it is possible that the crabs trimmed the colonies to their rounded shapes. All colonies are firm and rather hard in preservative, with spicules in a crowded layer in the surface test. The surface of the colony is raspy. Sometimes some sparse spicules are in the test around the zooids, but usually they are absent altogether and they are invariably absent from the central test core. A single layer of spicules is on the base of the colony. Spicules are regularly

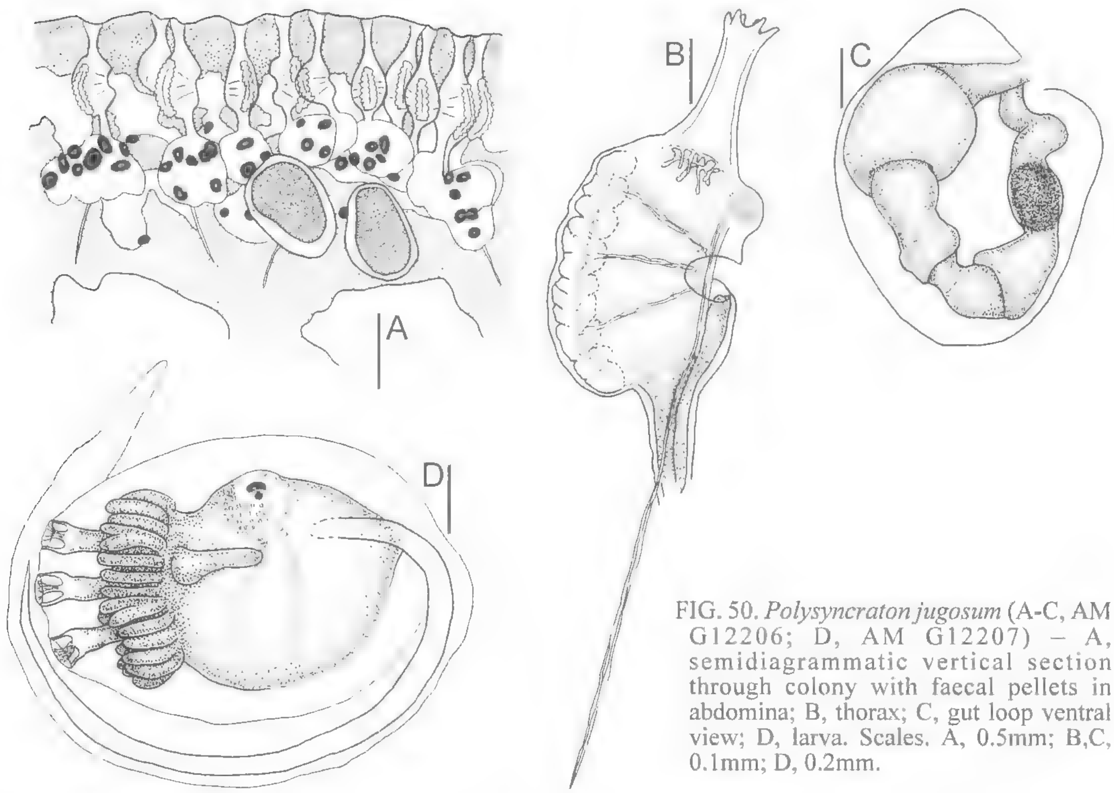


FIG. 50. *Polysyncraton jugosum* (A-C, AM G12206; D, AM G12207) – A, semidiagrammatic vertical section through colony with faecal pellets in abdomina; B, thorax; C, gut loop ventral view; D, larva. Scales. A, 0.5mm; B,C, 0.1mm; D, 0.2mm.

stellate, to 0.08mm diameter, with 7–9 conical pointed rays in optical transverse section. The ray length/spicule diameter ratio is 0.25. The common cloacal cavity is an extensive but relatively shallow space posterior to the zooids, separating the surface zooid-bearing layer of test (with its superficial crust of spicules) from the aspicular central test core. More restricted cloacal canals run between the zooids at thoracic level. Some test connectives attach the surface test to the central test core and embryos move through these connectives into the central core where they are incubated. It was not possible to remove zooids from the test, and they were examined in stained and cleared hand-cut sections of the whole colony

ZOOIDS. Zooids have long slender branchial siphons almost the same length as the relatively narrow thoraces. A sessile atrial aperture is across the dorsal mid-line of the pharynx. Round-tipped columnar epithelial cells project from the thorax. An atrial tongue was not detected. Six stigmata are in the two anterior rows in the pharynx, and this reduces to 5 in each of the posterior rows. A fine, tapering retractor muscle separates from the distal part of the oesophageal neck, just anterior to the stomach. The oesophageal neck is long and narrow, and the distal part of the gut loop is bent ventrally. The duodenum is long, expanded slightly at its distal end, and the posterior stomach is only slightly constricted off from the large proximal chamber of the rectum.

Testes were not detected in the newly examined specimens, although 4 spirals of sperm-filled vas deferens were found in zooids of AM G12205. Kott (1962) found testes with 8 follicles, probably in the zooids of AM G12207. Embryos and larvae are present in all the newly examined colonies but generally the latter are not well developed, the 3 anterior adhesive organs being the only trunk organs that could be detected. The only well developed larvae are in the central test of Newcastle Bight specimens (AM G12207). They are large, the trunk 1.3mm long, with the tail wound halfway around and about 10 long, narrow finger-like lateral ampullae, occasionally subdivided at their tips, on each side of the 3 antero-median adhesive organs. A large ocellus and an otolith are present, but generally adult organs are not well advanced in the oozooid — 4 rows of stigmata are beginning to form, as is the gut, but neither are conspicuous. There are no

blastozooids. A large external lateral ampulla projects horizontally back from the neck of the larva on the left side.

REMARKS. The species has similar colonies and zooids to *P. chondrilla* Michaelsen, 1924 from New Zealand which Kott (1962) had thought was the senior synonym. Kott (1962) thought that the New Zealand specimens differed from the Australian ones only in being single lobes with a single common cloacal aperture. However, single systems without side branches or multiple systems, can occur also in the Australian material (AM G12206). Nevertheless, the present species has larger spicules — those of the New Zealand species being only to 0.035mm diameter (Millar, 1982). *P. pedunculatum* from South Australia has similar colonies although they are stalked and aspicular, and the zooids have an atrial lip and retractor muscle from about halfway down the oesophagus. Spicules are a similar size to those of *P. infundibulum*, but they have fewer rays.

The form of these colonies, with their terminal cloacal apertures and posterior abdominal cavities separating the surface zooid-bearing layer of test from the central test core, occurs also in *Didemnum* (e.g. *D. roberti*, *D. molle*), *Trididemnum* (e.g. *T. nobile*, *T. caelatum*), *Leptoclinides* (e.g. *L. volvus*, *L. fungiformis*) and *Lissoclinum* (e.g. *Lissoclinum spongium*) and is known in this present genus in *P. pedunculatum* and *P. rica*.

Despite the lack of testes, atrial tongues, retractor muscles, and larval blastozooids in these long preserved specimens they reflect their affinity with *Polysyncraton* through the loosely coiled vas deferens, numerous, long, fine larval lateral ampullae on each side, long external projecting horizontal ampulla on the left side of the larval trunk and the lack of differentiation of adult organs in the larval oozooid.

There are 10 specimen lots of *Leptoclinum jugosum* listed as syntypes (Rowe & Marshall, 1979). However, only 4 specimen lots were examined in connection with the description of the species (Herdman & Riddell, 1913). These are from Manning Bight (Thetis Station 29, AM G12208), Port Jackson (Thetis Station 34, AM G12205), off Coogee (Thetis Station 44, AM G12206), and off Cape Three Points (Thetis Station 12, AM G12209). Kott (1962) referred the first (AM G12208) together with 3 others (AM Z1288, Z1290, Z1305) to *Didemum lambitum*. Thus AM G12205, G12206 and G12209 are the remaining syntypes. Of these, only AM G12209 has not been re-examined. Of the other 3 specimens (see Rowe & Marshall,1979), the specimen from Newcastle Bight (Thetis Station 22, AM G12207) was examined by Kott (1962) and found to be conspecific with one of the syntypes (AM G12205), but the further 2 specimen lots assigned to this species (AM Z1289, Z1301) remain to be re-examined. Kott's record of AM G12204 in this species is incorrect (Rowe & Marshall, 1979).

Polysyncraton lodix sp. nov.
(Figs 51, 163-I)

TYPE LOCALITY. Queensland (Whitsunday Passage, Deloraine I. 18m, coll. AIMS Bioactivity Group 13.10.87; holotype QM GH5751).

COLONY. The holotype colony is an extensive sheet, brown in preservative. Brown pigment is diffused in a thin, but uneven superficial layer of test (from which spicules are largely absent) in minute pigment cells scattered amongst the zooids, in their body walls (especially in the endostyle), in the wall of the gut and in a large brown egg in each abdomen. The variable thickness of the pigmented superficial layer of test may be the explanation of the dark patches on the surface of the photographed living specimen. A thin basal layer of spicule-free test up to one-third of the thickness of the lower part of the colony (in which abdomina are embedded) also has diffuse brown pigment in it. Stellate branchial apertures are evenly spaced over the upper surface, with 3 single rows of spicules projecting down in to the lining of the siphons. Common cloacal apertures are sessile, scattered over the upper surface about 1cm apart. Spicules are absent around the rims of these openings which appear brown owing to the diffuse brown pigment in the superficial layer of test. An extensive horizontal common cloacal cavity crossed by thoraces, each with a separate ventral sheath of spicule-filled test, lies beneath the thin surface layer of test.

With the exception of the superficial and basal layers of test, spicules are crowded throughout. They are large, often to 0.1mm diameter but occasionally larger (one spicule to 0.136mm diameter was detected), and stellate, with 9 –11 conical rays in optical transverse section.

ZOOIDS. Zooids are robust, to about 1mm long. Pointed columnar epithelial cells project from the whole surface of the zooid. The branchial siphon is short with 6 fine points around its rim. The atrial aperture is large, the parietal body wall being withdrawn to a narrow strip each side of the

endostyle. It flares out around the top of the thorax and exposes the whole branchial sac directly to the common cloacal cavity. A small circular lateral organ is depressed into the anterior part of the parietal body wall on each side where it flares out from the branchial sac. A narrow atrial lip projects from the centre of the anterior rim of the atrial aperture. It is often a short tongue-shaped projection but in the vicinity of a common cloacal aperture it becomes longer and has a bifid tip which spreads out and is incorporated in the rim of the common cloacal aperture.

The thoracic muscles are fine, with narrow dorsal pharyngeal and few delicate parietal longitudinal bands. A retractor muscle was not detected. The branchial sac has 10 rectangular stigmata in the anterior row, 9 in the second row and 8 in the third and fourth rows. Stigmata in the posterior row are shorter than in the other rows.

The gut loop is long with the distal post-pyloric part flexed ventrally and the gonads against the posterior surface of this flexure. Five male follicles have 4 coils of the vas deferens around them. The vas deferens does not pass around the outside of the ovum. Larvae are not known for this species.

REMARKS. The brown colour of the holotype, after more than 10 years in preservative, is conspicuous, apparently being not very different from the living colony. Other characteristics of the species are its capacious thoracic common cloacal cavity, numerous sessile common cloacal apertures, spicule-free layer on the base of the colony, small circular lateral organs, absence of a retractor muscle, and large stellate spicules.

Stellate spicules are not universal in this genus, the spicules often being burr-like or globular with numerous rays. *Polysyncraton* species with stellate spicules similar to the present species are *P. tegetum*, *P. regulum* and *P. arafurensis* (with more rays); *P. sideris* (with fewer rays); *P. jugosum* and *P. orbiculum* (with smaller spicules, some with differently shaped rays); and *P. echinatum*, *P. rubitapum* and *P. pseudorugosum* (with smaller spicules). Of these, *P. pseudorugosum* most closely resembles the present species in other characters viz. spicules throughout the colony, shape of the thoraces and the lateral organ and spicule shape. It differs in the cloacal cavity with zooids along each side of circular cloacal canals, a retractor muscle, and a limited range in spicule size.

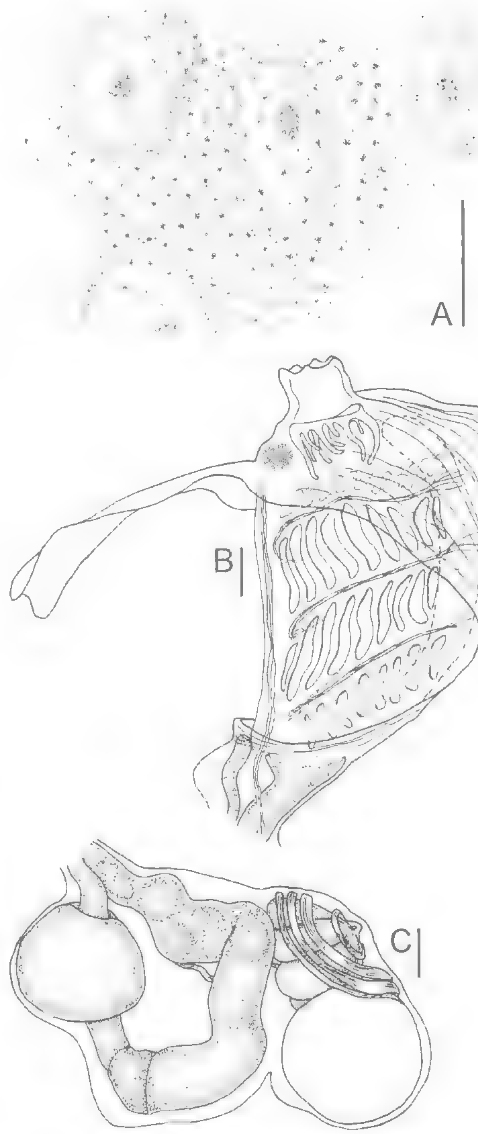


FIG. 51. *Polysyncraton lodix* sp. nov. (QM G5751) – A, surface of colony; B, thorax; C, abdomen ventral view. Scales: A, 0.5cm; B,C, 0.1mm.

Polysyncraton magnetae Hastings, 1931
(Figs 52, 162-I)

Polysyncraton magnetae Hastings, 1931: 100. Kott, 1962: 303; 1998: 90.

Not *Polysyncraton magnetae*: Millar, 1963: 702.

NEW RECORDS. Queensland (Heron I., QM G301538, G308197).

PREVIOUSLY RECORDED. Queensland (Low Is – holotype AM G13485 Hastings 1931).

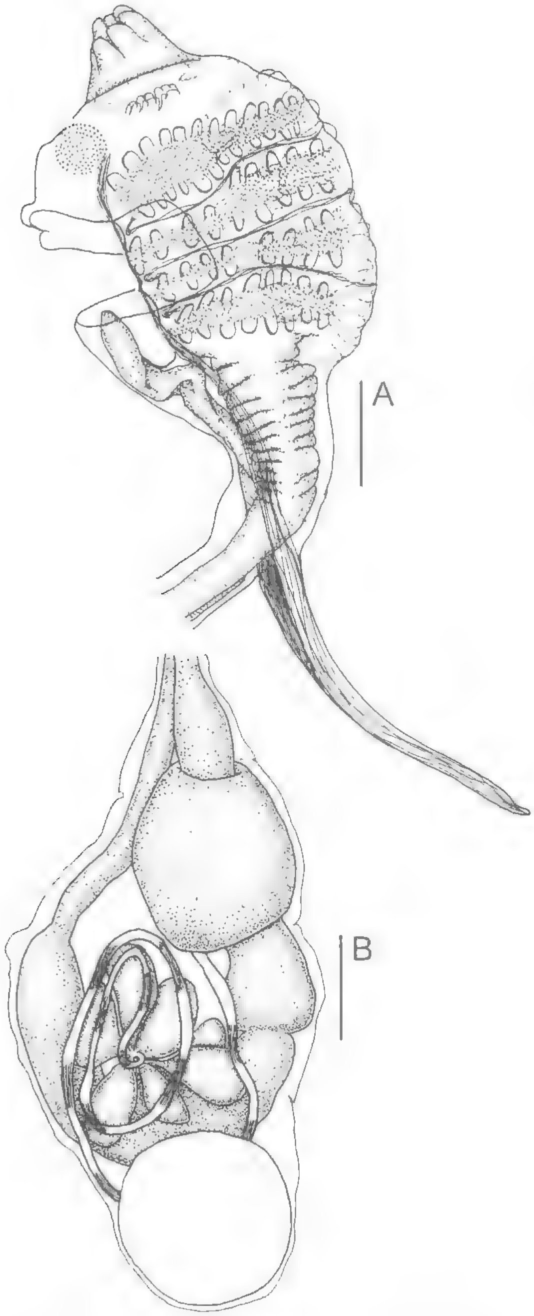


FIG. 52. *Polysyncraton magnetae* (QM G308197) – A, thorax; B, abdomen. Scales: 0.2mm.

COLONY. Colonies are quite solid, encrusting sheets with spicules throughout. A superficial layer of bladder cells is conspicuous, especially around the margins of the colony. Zooids are in double rows, along each side of the cloacal canals that surround circular areas of zooid-free test. Their ventral surfaces embedded around the margins of the solid zooid-free areas, have only the dorsum of each thorax exposed to the cloacal canals.

Spicules are small, to 0.035mm diameter, sometimes globular, with flat-tipped, long, cylindrical rays, although others have rounded or pointed tips and some have long conical pointed rays, about 15–17 in optical transverse section.

In preservative colonies are white, stomach and intestine yellowish-green, thoraces white and eggs bright yellow. In life the colonies are white and opaque, with some patches of *Prochloron* on the surface.

ZOOIDS. Zooids are moderately large, the thorax and abdomen together (including a long oesophageal neck) are about 1.2mm long. The branchial siphon is relatively short with 6 lobes around the rim. A short retractor muscle projects from a short distance down the oesophageal neck. The gut loop is long, with the usual subdivisions of stomach, and short mid-gut between the long duodenum, and the rectum. The proximal part of the ascending limb of the loop, i.e. the proximal part of the rectum, is curved ventrally over the gonads. The large testis has 8 or 9 follicles in a long, grape-like cluster. The vas deferens makes 3 spirals on its surface. The ovary is between the outside coil and the inner coils and, as the egg develops, the vas deferens is pulled out across its surface, tending to distort the inner coil and pull it over so that it is hooked over the centre of the testis. Larvae are not known for this species.

REMARKS. The species is characterised by its superficial layer of bladder cells, small spicules (some globular and some stellate), and the relatively large zooids along each side of cloacal canals surrounding zooid-free test areas. Hastings (1931) referred to small (0.03mm diameter) globular spicules. Apparently she overlooked the stellate ones. The cloacal systems, testis and vas deferens coils of the newly recorded specimens are similar to those described by Hastings (1931) from Low Is.

The 3 specimens from Australia assigned to this species by Millar (1963: see *P. meandratum*) have small burr-like globular spicules rather than the characteristic variety of stellate and globular ones and they do not have zooids along each side of cloacal canals as in the present species. *P. otuetue* Monniot & Monniot, 1987 has predominantly stellate spicules with pointed conical rays like those in the present species,

although its colonies are different and it lacks the globular spicules and the ones with round-tipped rays that also are present in *P. magnetae*. *P. pavimentum* Monniot, 1993 has a similar range of spicules to the present one, but they are larger, the spicule rays are generally much shorter than in the present species and the colony has isolated groups of zooids around central common cloacal apertures. *P. dromide* has a colony similar to the present one, with circular canals lined by zooids surrounding zooid-free areas. The species are distinguished mainly by the distribution of the spicules and by the length of the branchial siphons. *P. pseudorugosum* also has a colony with zooids along each side of the cloacal canals that surround zooid-free raised areas of test. The present species differs in having 3 coils of the vas deferens (rather than 4) and a larger thorax with the retractor muscle from halfway down the oesophageal neck (rather than at the top).

Polysyncraton meandratum Monniot, 1993
(Figs 53, 162B; Pl. 5F)

Polysyncraton meandratum Monniot, 1993: 6.
?*Polysyncraton magnetae*: Millar, 1963: 702.

NEW RECORDS. Queensland (Caloundra, QM G308460; Capricorn Group QM G308100, G308106, G308217).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1993).

COLONY. Colonies are thin sheets with a conspicuous superficial bladder cell layer creating a smooth upper surface. A layer of brown pigment beneath the bladder cell layer is more intense around each branchial aperture. A few scattered spherical pigment cells are in the test, but more often they are in the body wall of the zooids. A thin layer of crowded spicules is beneath the bladder cells and forms a sort of tent over each zooid which is perforated by the branchial aperture. Three to 6 small groups of spicules in the siphonal lining are seen from the surface in the stellate branchial apertures or a line of spicules lines the openings. Spicules are absent from other parts of the colony which is packed with bladder cells. The layer of spicules (which is in the roof of the common cloacal cavities) is interrupted around the cloacal apertures and these spicule-free areas often are lens-shaped or fusiform and radiate out along the deeper primary cloacal canals that surround each clump of zooids. Thoracic cloacal cavities are extensive, the thoraces crossing them independently in a strip of test. The abdomina are embedded in the thin translucent basal test. Juvenile colonies have common cloacal canals that branch and form contiguous circles. These canals have zooids along each side of the canals and the surface test is depressed over them. Living colonies are a slightly iridescent brown colour with ferruginous[R] zooids showing through the spicules. Colonies are white in preservative.

Spicules are never larger than 0.05mm in diameter, globular or burr-shaped with more than 20 rays in optical transverse section, often with flat, but sometimes pointed or chisel-shaped tips.

ZOOIDS. Zooids are about 1.5mm when partially relaxed, and the thorax is then twice the length of the abdomen. More often they are contracted and both abdomen and thorax are about the same size. Small rounded projecting columnar cells are on the anterior part of the thorax. Six distinct branchial lobes surround the incurrent aperture. The atrial aperture is large and sessile exposing most of the branchial sac directly to the cloacal cavity. A long forked atrial tongue with fine longitudinal muscles projects from the anterior rim of the atrial aperture. The lateral organ is a relatively small saucer about 0.04mm diameter. The thoraces of the newly recorded material are usually contracted, and the longitudinal muscles on the parietal body wall and the transverse muscle bands in the branchial wall are strong and conspicuous. A retractor muscle of varying length projects from the posterior end of the thorax. The gut loop is bent up alongside the oesophageal neck. It has the usual large rectal chamber separated from the distal end of the gut by a narrow tube. Three coils of the vas deferens surround 3 or 4 male follicles.

Larvae were not taken in the Australian material. They are known from New Caledonia (Monniot, 1993). The larval trunk is only 0.43mm, a blastozooid is present, and 8 lateral ampullae are along each side of the 3 median adhesive organs. An external lateral ampulla is not reported, although very likely it is present on the left side of this large characteristic larva.

REMARKS. The types from New Caledonia appear to have the same number of vas deferens coils, and 4 or 5 rather than 3 or 4 testis follicles. They have the same transparent superficial layer of test, with a patchy layer of spicules beneath it. The New Caledonian specimens also appear to have a muscular thorax, and a strong retractor muscle like the newly recorded ones.

P. meandratum has some resemblance to *P. magnetae* Hastings, 1931 from Low Is. Both have bladder cells in the floor of the cloacal

cavity and in the surface layer of test, quite small globular spicules with long, cylindrical, flat-ended rays, and zooids are along each side of thoracic (or deeper) cloacal canals. However, *P. meandratum* has no spicules in the lower half of the colony, while *P. magnetae* has; and in *P. magnetae* the primary cloacal canals surround zooid-free stands of test, while in *P. meandratum* they surround groups of zooids. Further, the spicules of the present species (to 0.05mm diameter) are larger than those of *P. magnetae* (to 0.035mm diameter) and spicules with conical pointed rays are common, while in *P. meandratum* they are not.

Like the present species, *P. circulum* lacks a superficial bladder cell layer and also has some similar spicules. However its spicules are larger, and stellate ones with conical pointed rays as well as the globular ones occur. In *P. rugosum* the spicules are similar but they are uniformly distributed through the colony, and the larvae have more lateral ampullae.

Monniot (1993) drew attention to similarities between the present species and *P. otuetue*. This is confirmed by the present study. Both species have similar zooids with 4 coils of the vas deferens and both have similar fleshy colonies with a single layer of spicules beneath the bladder cells. *P. otuetue* differs in its stellate spicules with relatively few pointed conical rays. The present species also resembles *P. purou*, with spicule-free areas around common cloacal apertures and brown or ferruginous[R] zooids. The stellate spicules of the latter species, its fewer vas deferens coils, and the orange colour of the living colony distinguish it. *P. arafurensis* resembles the present species in having 3 vas deferens coils, 5 or 6 male follicles, bifid atrial lip, and thin colonies. However, it has spicules crowded throughout the colony and lacks the blunt-tipped rays that sometimes occur in *P. meandratum*.

P. discoides has similar, but smaller spicules, similarly distributed. *P. papyrus* also has similar but smaller spicules, although they are crowded throughout. Neither *P. discoides* nor *P. papyrus* have the conspicuous bladder cells layer of the present species. The younger colonies with zooids along each side of circular canals resemble *P. dromide* but spicules are different. The species also resembles *P. fuscum* Nott, 1892 from New Zealand (Hauraki Gulf) and it is possible that it is conspecific, other tropical species being known from the North I. (see *P. rugosum*). *P. magnetae*: Millar, 1963, from

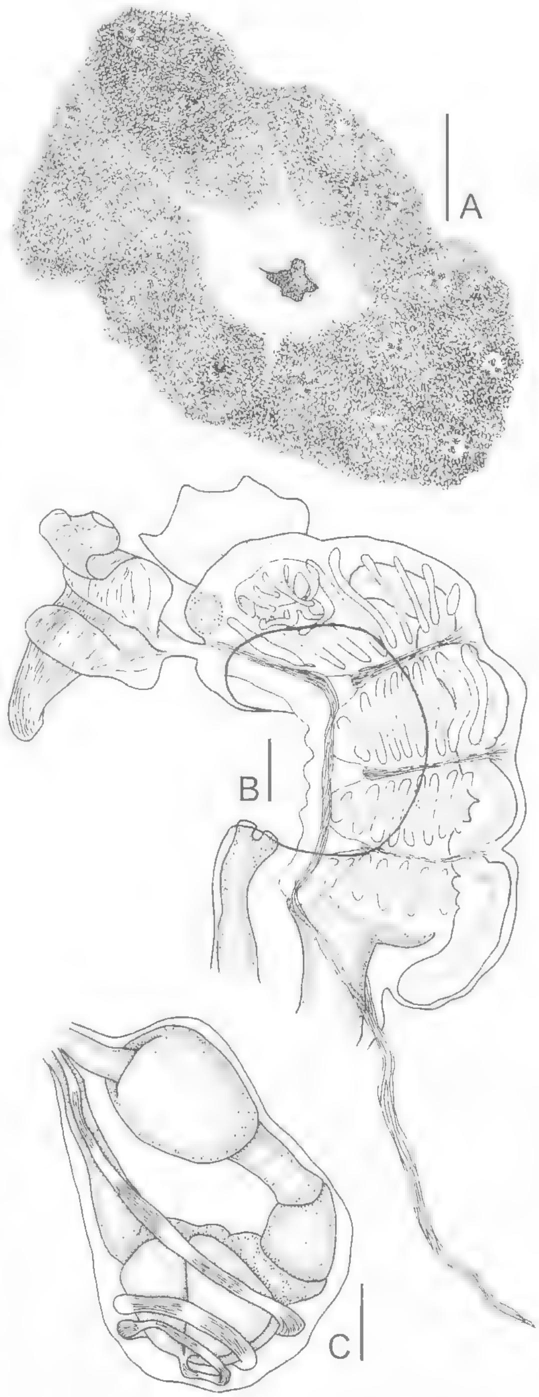


FIG. 53. *Polysyncraton meandratum* (A, QM G308217; B, QM G308460; C, QM G308100) – A, colony showing common cloacal aperture in the centre of a clear spicule-free area of test; B, thorax showing large bifid atrial tongue; C, abdomen. Scales: A, 1.0mm; B,C, 0.1mm.

Australia (location unknown) has similar burr-like spicules confined to a layer beneath the surface, and a similar larva with 8 pairs of lateral ampullae and cannot be distinguished from the present species.

Polysyncraton millepore Vasseur, 1969
(Figs 54, 164H; Pl. 5G)

Polysyncraton millepore Vasseur, 1969: 917. Monniot, F. & Monniot, C., 1997: 10.
Polysyncraton thallomorpha Monniot, 1993: 14

NEW RECORDS. Queensland (Whitsunday Is, QM G302945).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1993). Western Indian Ocean (Madagascar – Vasseur 1968; Mozambique, Tanzania, Northern Natal – Monniot, F. & Monniot, C., 1997).

This species is one of few with a range from the West Indian Ocean to the West Pacific.

COLONY. Colonies are extensive thin, hard, even, encrusting sheets, about 4mm thick with smooth and rounded edges, that curl up when removed from the substrate. The flat upper surface of the newly recorded specimen is shiny and black in life and becomes blotchy brown and white in preservative. Brown colour is especially in the vicinity of the branchial apertures and, in some parts of the colony, in the surface test where it is depressed around white, zooid free slightly elevated oval and rounded areas. The African specimens have various mottled patterns black, brown and grey in life (Monniot, F. & Monniot, C., 1997). The base is always white, opaque with fine ripple marks on the hard surface which is said to be difficult to remove from the substrate. Zooids sometimes open along each side of primary cloacal canals that surround elevated areas of zooid-free test or clumps of zooids. Cloacal spaces penetrate in amongst the zooids at thorax level sometimes isolating thoraces from one another, each in a spicule-filled ventral sheath of test. Oval to elongate clumps of spicules associated with the lateral organs are on the edges of these thoracic sheaths. The surface layer of test is thin and the basal layer slightly thicker, containing the small embedded abdomina and developing larvae. Common cloacal apertures are fairly evenly spaced about 1cm apart, just inside the outer margin of the colony and some are randomly scattered over the rest of the upper surface. They are closed in the available colonies, with the rim of the opening slightly gathered in. About 6 spicule-filled ribs of test can be seen inside these apertures and the tips of atrial tongues fit into the test around the rim of the opening between these ribs. Small white dots over the surface are formed by plugs of crowded spicules in the branchial siphons.

Spicules are crowded throughout the colony packed especially firmly in the thin, even, basal layer beneath the embedded abdomina. They are to 0.05mm diameter, with 11 to 13 sharply pointed or truncated flat-tipped conical rays. The ray length/spicule diameter ratio is about 0.28.

ZOOIDS. Zooids are about 1.5mm long, with the abdomen about half the length of the thorax. The branchial siphon is large, almost half the length of the branchial sac and sometimes tulip-shaped. Six sharp points are around the rim of the opening. The atrial tongue is of variable length and shape, depending on the position of the zooids in relation to the common cloacal aperture. Zooids in the vicinity of these openings have long atrial tongues slightly concave or assymmetrical across the tip where they are incorporated into the test around the apertures. Generally, however, zooids have small, straight, narrow, atrial tongues, slightly spatulate at the tip. Although some of the longer ones are flat or concave at the tip, Bifid atrial tongues have not been detected in this species. Small projecting columnar epithelial cells are conspicuous, especially toward the tips of the atrial tongues, and are conspicuous also down the ventral border of the zooid. The branchial sac has 8 long stigmata in the anterior row. Stigmata were not counted in other rows, although the posterior row appears to be shorter than the others. A long tapering retractor muscle projects back from the middle of the oesophageal neck. The gut forms the long curved loop usually found in this genus.

In the newly recorded specimen, even though well advanced embryos are present in the base of the colony, only 3 zooids were found to have mature testes. They consist of 2 or 3 follicles, surrounded by 5 coils of the vas deferens. It is possible that the species is protandrous.

The larval trunk is robust, oval and about 0.9mm long, with 24 ectodermal ampullae forming a corona around the 3 antero-median adhesive organs. A large horizontal lateral ampulla projects posteriorly from the constricted waist between the adhesive apparatus and the developing oozooid on the left side of the trunk. The cerebral vesicle with otolith and ocellus is well developed, but the pharynx is not perforated. A vertical gut loop appears to be differentiating and a large spherical reservoir of yolk is just in front of it.

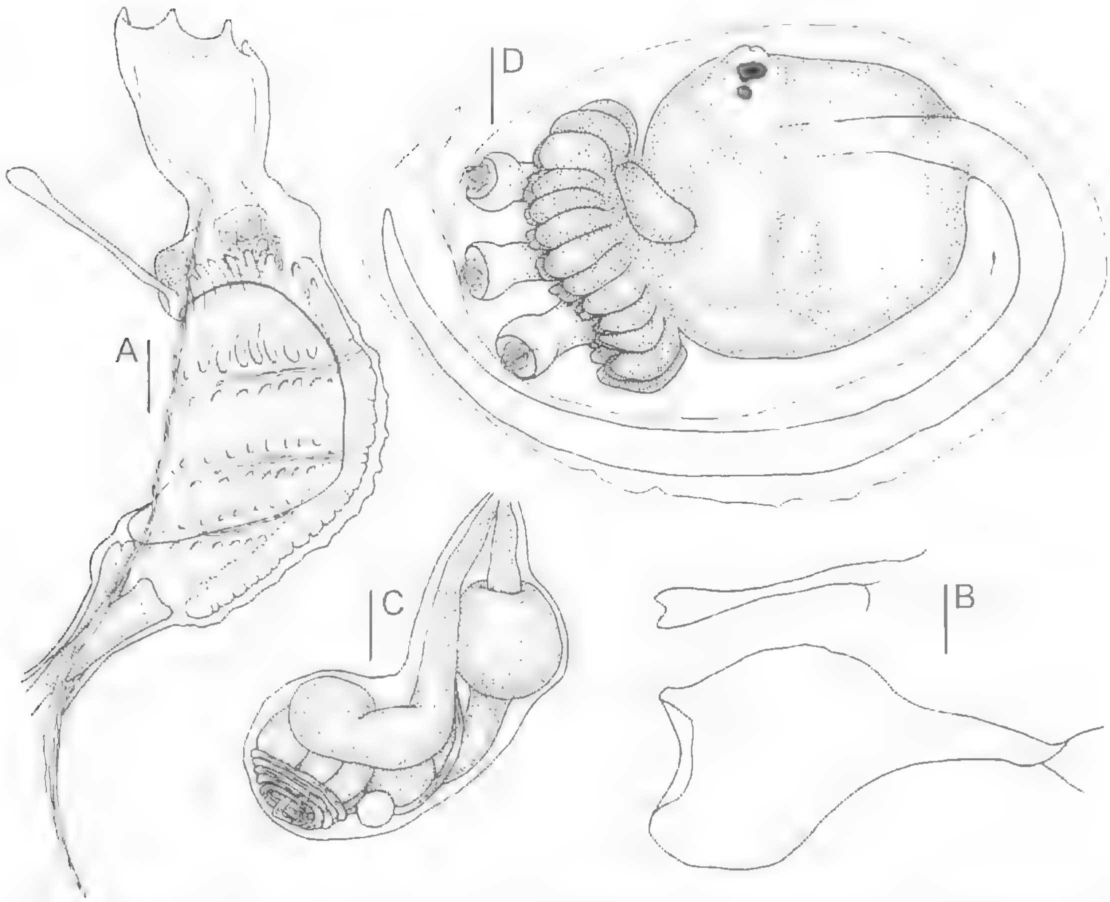


FIG. 54. *Polysyncraton millepore* (QM G302945) – A, thorax; B, various atrial tongues; C, abdomen; D, larva. Scales, 0.1mm.

REMARKS. *P. arafurensis* has similar but slightly larger spicules with more numerous points, a similar zooid, and a hard colony with a smooth even surface. However *P. arafurensis* has only 3 coils of the vas deferens, 7–9 testis follicles, a wider and more distinctly subdivided atrial lip and it lacks the hard, rigid basal test of the present species. *P. pseudorugosum* has similar larvae, although the adult organs in the trunk are more advanced, the colony surface and common cloacal systems are different and it lacks spicules with truncated rays. The zooids also resemble those of the temperate *Didemnum bicolor* and *D. ossium* which both have tulip-shaped branchial apertures. Although they can be distinguished by their posterior abdominal cavities as well as their generic characters. *Leptoclinides durus* and *L. uniorbis* Monniot & Monniot, 1996 both have a finely rippled base like the present species but are distinguished by their generic characters.

Specimens from New Caledonia conform with other known material in all respects except that the vas deferens appears to have one more coil, although only 4 or 5 coils are reported (Monniot, 1993: fig. 7). Specimens from the western Indian Ocean apparently differ from the Pacific Ocean ones in surface colour, which is notoriously variable. Otherwise colonies and zooids are identical.

Polysyncraton multiforme sp. nov. (Figs 55A-E, 163D; Pl. 5H)

TYPE LOCALITY. Western Australia (Houtman's Abrolhos, coll. C.Bryce, holotype QM G304641, paratype QM G304673).

COLONY. The type colonies are tough, massive and irregular cones, or mushroom-shaped lobes, or lamellae, sometimes branching off one

another. The firm spicule-free test mass in the centre of each lobe is filled with large crowded bladder cells (about 0.08mm diameter). The thin outer layer of the colony has a layer of spicules superficially and this is penetrated by the branchial siphons of the zooids, which lie just beneath it. Branchial apertures are stellate with a margin of spicules. Spicules are present only in the superficial layer of test, at the surface of the colony. They are stellate, to 0.05mm in diameter with long pointed to blunt-tipped rays, 17–19 in optical transverse section.

Large embryos are being incubated just posterior to the zooids. A horizontal cloacal cavity is at mid-thorax level. Up to 80 zooids are grouped in more or less circular areas, each group isolated from others by a narrow zooid-free ring of test. Horizontal common cloacal chambers expand into deeper cavities in the centre of each group of zooids, beneath a large common cloacal aperture, although these openings were not always detected. The rims of the common cloacal apertures are also divided into 6 lobes.

ZOOIDS. Zooids are small, the abdomen slightly larger than the thorax, but only about 0.8mm long. The 6 branchial lobes are fine and pointed, and a long, narrow atrial tongue (bifid at the tip) projects from the anterior rim of the large aperture. Crowded, tapering columnar cells project from the anterior part of the thoracic wall. A very short, stout retractor muscle projects from the posterior end of the thorax. Ten short stigmata are in the anterior row in the small branchial sac, and 8 were counted in the posterior row. The gut loop is open. The duodenum is relatively short, and a balloon-like mid-gut meets the rectum in the pole of the loop. Opposite the stomach a narrow constriction surrounded by conspicuous tubules of the gastro-intestinal gland distinctly separates the wide proximal part of the rectum from the narrow distal part. Gonads were not detected in either of the available specimens, although many embryos are being incubated.

Larvae (in both holotype and paratype) are large, with the trunk 0.9mm long and particularly deep. The 3 large antero-median adhesive organs have 16 short blunt lateral ampullae on each side. An otolith and ocellus are in the cerebral vesicle and the gut forms a vertical loop. No other larval or developing adult organs could be detected in these large, opaque larvae. The tail is wound about two-thirds of the way around the trunk.

REMARKS. These bulky colonies, with their massive central test packed with bladder cells, are very different from the thin investing sheets, or gelatinous cushions so often encountered in *Polysyncraton* from shallow tropical waters. Although gonads are not developed in the type material the large, unusually robust larvae with numerous lateral ampullae, small retractor muscle and long atrial tongue are characteristic of the genus. The separate systems resemble *P. glaucum* but the present species has more numerous spicule rays and bulky colonies. The New Caledonian *P. pavimentum* Monniot, 1993 also has similar systems but less bulky colonies, spicules with fewer rays and more larval ampullae. *P. lithostrotum* from New Zealand also has isolated systems but short rounded spicule rays.

In its large colony with spicules in the surface test but largely absent from the central core, this species may be thought to resemble *P. jugosum*, but the cloacal systems are entirely different. The spicules and some aspects of the zooids and larvae resemble *P. oceanium* but it has a thin (rather than massive) colony, spicules are present throughout and it lacks the isolated systems of the present species. Spicules also resemble those of *P. purou*, but the latter species has a superficial layer of bladder cells, and different systems from the present species.

The bladder cells crowded throughout and the single layer of spicules at the surface are reminiscent of *D. chartaceum*, which also has an atrial tongue, but its almost globular spicules with short rays and unique systems help to distinguish it.

Polysyncraton oceanium sp. nov.
(Figs 55F,G, 164A; Pl. 6A)

Polysyncraton dohboense: Kott, 1981: 176.

TYPE LOCALITY. Fiji (Great Astrolabe Reef, Dravuni, low tide rubble fauna, coll. P. Kott July 1980, holotype QM GH143).

NEW RECORDS. Queensland (Heron I., QM G308203).

COLONY. The colony is a flat sheet with a thick superficial bladder cell layer. Spicules, crowded beneath the bladder cells, become less crowded in the remainder of the test and generally are not present around the thoraces. Zooids are arranged in clumps, with a deep cloacal cavity surrounding each clump and thoracic canals penetrating amongst the zooids. In life cloud-like patches of brown pigment cells are embedded in the bladder cell layer, and in some places fine veins of brown pigment appear to interrupt the spicules in the surface test. An open meshwork of opaque yellow pigment appears to divide the surface into

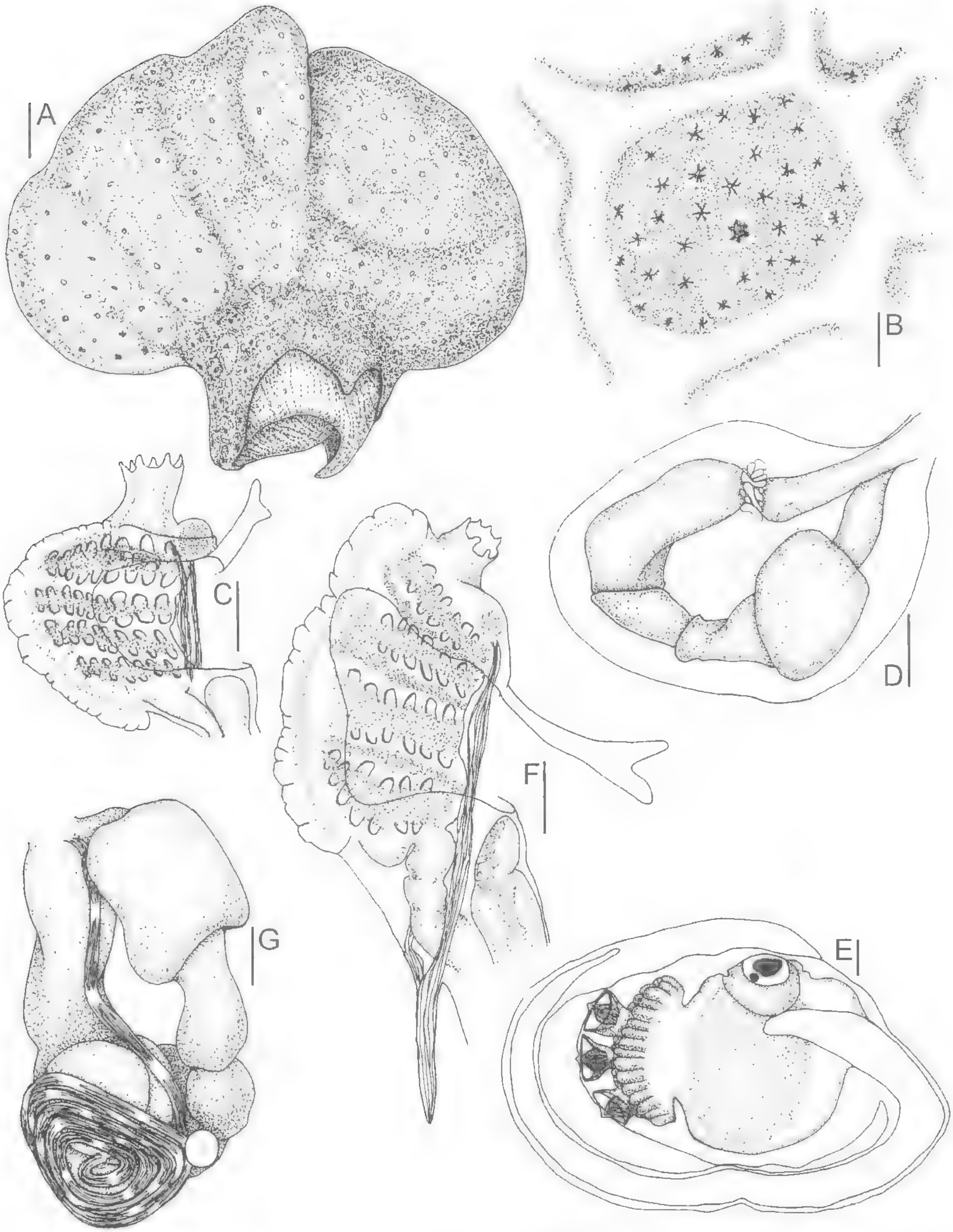


FIG. 55. A–E, *Polysyncraton multiforme* sp. nov. (A, QM G304673; B, QM G304641) – A, colony; B, part of surface showing a single system with the central common cloacal aperture surrounded by branchial apertures; C, thorax; D, abdomen; E, larva. F, G, *Polysyncraton oceanium* sp. nov. (QM GH143) – F, thorax; G, abdomen. Scales: A, 1.0cm; B, 2.0mm; C–G, 0.1mm.

polygonal areas but these are not associated with cloacal systems. Some green *Prochloron* is on the surface. The dark, burnt carmine zooids are visible through the stellate branchial apertures. The cloacal apertures are randomly spaced over the surface and brown pigment is present around their rims. In preservative the colonies are white, and clumps of zooids cause elevations on the surface.

Spicules, up to 0.05mm in diameter, line the branchial siphons and outline the stellate apertures. Most have 15–19 conical, pointed rays in optical transverse section but some are globular with round-tipped rays.

ZOOIDS. Zooids are small, to about 1mm long. The branchial siphon is short and cylindrical. The atrial opening is large and has a bifid tongue, of variable length, from the upper rim of the opening. A lateral organ is on each side of the thorax. A retractor muscle projects from halfway down the oesophagus. The gut loop has the usual rounded stomach, bulbous duodenum, small mid-gut and wide proximal and narrow distal parts of the rectum.

Gonads are in the type specimen. The vas deferens coils 6 times around 2 or 3 testis follicles. Larvae are not known. Neither gonads nor embryos occur in newly recorded specimen,

REMARKS. *P. oceanium* has, like *P. pavimentum* (Monniot, 1993) from New Caledonia, stellate spicules with numerous conical pointed as well as flat-tipped rays and some globular ones to 0.05mm diameter, a large atrial tongue, 2 male follicles and 6 coils of the vas deferens. However, *P. pavimentum* is distinguished by the distinct polygonal systems isolated from one another by zooid free test that is not penetrated by cloacal canals, and by a small retractor muscle projecting from the posterior end of the thorax or absent altogether. The stellate spicules of *P. multiforme* have longer and more pointed rays and it also has isolated systems. *P. purou*, is similar but its spicules have longer, more numerous, and not such regularly conical rays

The fine lines Kott (1981) refers to are not as regular as she implied. They appear to be the 'veins' of pigment interrupting the surface spicules seen in the living specimen (QM G308203). The surface depressions over the deeper cloacal canals around each clump of zooids create a mosaic of raised areas on the surface of the colony that are emphasised by the disposition of yellow opaque pigment in the surface test.

On re-examination *D. grande*: Kott, 1962 from Rottnest I. (AM Y1514) is found to be a (probably undescribed) *Polysyncraton* sp. Its spicules resemble those of the present species but the thin sheet-like colony with spicules crowded throughout appears to be in vegetative phase, lacking any common cloacal cavity. The small zooids are embedded in the test amongst the spicules. The thoraces appear to be rudimentary vegetative ones and the abdomina are small but sexually mature with the 3 or 4 testis follicles spent and the 4 coils of the vas deferens packed with sperm. The bladder cell layer (present in *P. oceanium*) does not occur. Although it probably is an undescribed species, there is insufficient information available from this specimen to erect a new species (see also *P. palliolum* Remarks).

Polysyncraton orbiculum Kott, 1962
(Figs 56A, 162F)

Polysyncraton orbiculum Kott, 1962: 300 (part, specimens from Mary Cove, Salmon Bay and Port Noarlunga); 1972a: 21; 1976: 72; 1998: 90.

PREVIOUSLY RECORDED. Western Australia (Rottnest I., Mary Cove coll. P. Kott January 1948, holotype AM Y1486; Salmon Bay, inner pool, coll. P. Kott 18.11.51, paratypes AM Y1479). South Australia (Rapid Head – SAM E2637-8 Kott, 1972a; Port Noarlunga – AM Y1484 Y1485 Kott, 1962). Victoria (Western Port – Kott, 1976).

COLONY. Colonies are thin, flexible and sheet-like. Spicules are crowded throughout the colony, interrupted by a ring of about 8 vesicles around each branchial aperture. Spicules are to 0.05mm in diameter, stellate, generally with conical or blunt-tipped club-shaped rays. The ray length/spicule diameter ratio is 0.25 and 9–11 rays are in optical transverse section. Spicules outline the stellate branchial apertures. The cloacal cavity is horizontal and thoracic and the thoraces cross it in a separate sheath of test. Abdomina are embedded in the basal test. Pigment particles are mixed with the spicules in surface and basal test. Zooids, with brown squamous epithelium on their body walls, are seen through the layer of spicules in the surface test.

ZOOIDS. Zooids are small. The atrial aperture is wide, exposing most of the branchial sac to the cloacal cavity and an atrial tongue projects from its anterior border. The short branchial siphon has 6 pointed lobes. About 8 stigmata are in each of the 4 rows in the branchial sac. The gut is divided into the usual stomach, duodenum, mid-gut and

proximal and distal parts of the rectum. The testis is divided into 4 or 5 follicles and has 5 coils of the vas deferens around it. Large yellow eggs are in the abdomina of some specimens, but larvae are not known for this species. The larva figured by Kott (1962, Fig. 35) is from the type specimen of *P. sideris* sp. nov.

REMARKS. Other specimens from Rottnest I. assigned to this species by Kott (1962: AM Y1480, Y1483, Y1487) with large (to 0.1mm or more diameter) spicules, long acutely pointed spicule rays and radial ribs of spicules around the common cloacal apertures are a different species — *P. sideris*. Despite its small zooids which, like the colonies, resemble those of *Didemnum delectum*, the species is assigned to *Polysyncraton* on the basis of its gonads, its large, yellow eggs and the vesicles interrupting the spicules in the surface test like those of *P. circulum* and *P. sideris*. The species is distinguished from the former by its stellate spicules, and from the latter by its smaller spicules (up to 0.05mm diameter) with club-shaped as well as conical rays. *P. arafurensis* has some similarities to the present species, but it has larger spicules with more and longer, more acutely pointed rays. *P. orbiculum* is distinguished from *P. paradoxum* Nott, 1892 (from New Zealand) and *P. rugosum*, by its stellate spicules, fewer testis follicles and brown squamous epithelium.

Polysyncraton otuetue Monniot & Monniot, 1987
(Figs 56B, 164C; Pl. 6B)

Polysyncraton otuetue Monniot & Monniot, 1987: 45.

NEW RECORDS. Queensland (Swain Reefs, QM G308378).

PREVIOUSLY RECORDED. French Polynesia (Monniot & Monniot, 1987).

COLONY. Colonies are fleshy, gelatinous plates, with a thick superficial layer of bladder cells mixed with orange to brown cells, sometimes in clouds, and sometimes especially crowded around the branchial apertures. Spicules are in a layer beneath the bladder cells and beneath and around clumps of zooids, but are, at most, only sparse in the remainder of the test. They are absent from the rims of the common cloacal apertures and are never present in the floor of the common cloacal cavities or in the base of the colony. Spicules (to 0.085mm diameter) are stellate, all with 13–15 sharply pointed conical rays in optical transverse section. The ray length/spicule diameter ratio is 0.25. Common cloacal apertures are large, and the common cloacal cavities sometimes extend posterior to the zooids.

In life, colonies are bright orange[R], and the zooids are chinese orange[R] or brownish red or seal brown[R]. The dark zooids show through the open branchial apertures. In preservative, the colonies are orange, and the zooids are pale orange to colourless.

ZOOIDS. Zooids are small. The branchial aperture on a short siphon has 6 pointed lobes around the rim. The atrial aperture has a small bifid atrial lip. About 10 stigmata are present in each of the 4 rows of the branchial sac. The lateral organ is small, in the anterior third of the thorax, and the retractor muscle is free from about halfway down the oesophageal neck. In the newly recorded material 4 testis follicles are surrounded by 4 loose coils of the vas deferens. Although the same number of coils were present in the French Polynesian material, there were up to 8 testis follicles. Larvae are not known for this species.

REMARKS. Colonies resemble those of *P. meandratum* and *P. purou* but the large, uniformly stellate spicules with relatively short, pointed conical rays distinguish it, the spicules of *P. meandratum* being uniformly burr-like and globular, and those of *P. purou* being diverse, some with long crowded club-shaped to almost fusiform and flat-tipped rays and others with shorter pointed conical rays. Spicules resemble those of *P. arafurensis* but have fewer and shorter rays. The rays are more numerous than in the spicules of *P. echinatum*. Spicules of *P. scobinum* are a similar size, but are crowded throughout and the spicule rays are not all uniformly pointed.

Polysyncraton palliolum sp. nov.
(Figs 56C-E, 163B; Pl. 6C)

TYPE LOCALITY. Western Australia (Rottnest I., 0.5 n miles off Charlotte Point, 18 m AIMS Bioactivity Group 14.3.89, holotype QM G300988).

COLONY. The holotype colony is a robust oval slab, about 6cm long, up to 3cm wide and about 0.5cm thick. The upper surface is flat and has a mosaic of low, oval (5mm long) elevations separated from one another by depressions over the deep primary cloacal canals which have zooids opening along each side. The base of the colony is turned up and slightly rolled in around the outer margin forming a firm rounded border that frames the flat upper surface. The position of the branchial apertures is indicated by a plug of spicule-filled test in each branchial siphon but the

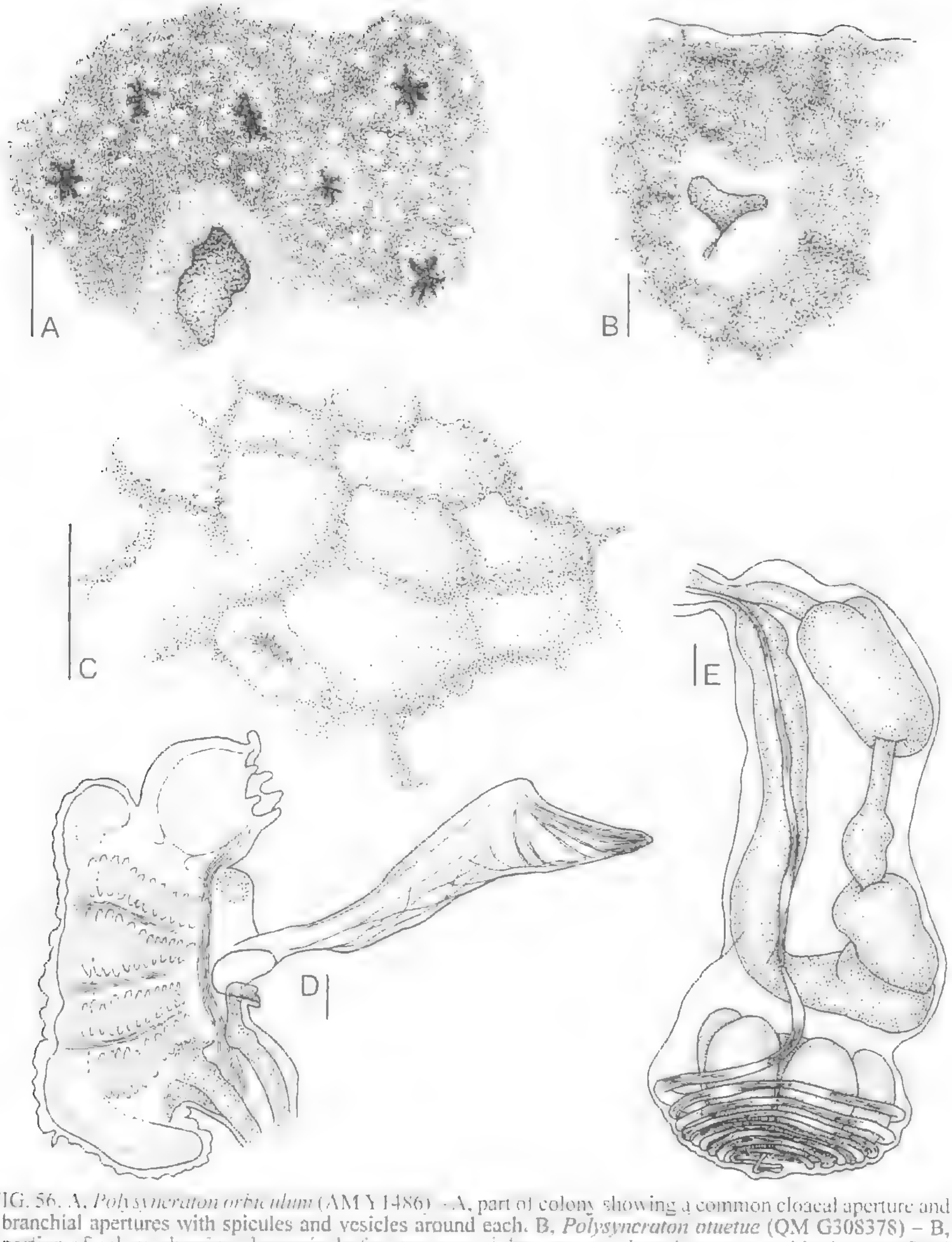


FIG. 56. A, *Polysyncraton orbiculum* (AM Y1486) – A, part of colony showing a common cloacal aperture and branchial apertures with spicules and vesicles around each. B, *Polysyncraton otuetue* (QM G308378) – B, portion of colony showing clear spicule-free test around the common cloacal aperture and in the superficial layer of test. C–E, *Polysyncraton palliolum* sp. nov. (QM G300988) – C, surface of colony; D, thorax; E, abdomen. Scales. A, 0.5mm; B. 1.0mm; C, 5.0mm; D,E, 0.1mm.

openings do not appear to be stellate. Spicules are evenly spaced throughout but are not very crowded, the colony being firm and tough but not hard or brittle. Spicules are of moderate size (to 0.06mm diameter) with 17–19 long, usually pointed, conical or slightly flattened and occasionally flat-tipped rays in optical transverse section. The ray length/spicule diameter ratio is 0.35.

Primary common cloacal cavities are deeper than the length of the zooids but do not extend horizontally behind them. Randomly spaced, frilled common cloacal openings are on low rounded elevations over larger cloacal spaces that also are surrounded by zooids. The arrangement of zooids alongside the cloacal canals is equally apparent in living and preserved colonies. The living colony is a pink colour. In preservative it is white.

ZOOIDS. Zooids are relatively large, to nearly 2mm long, with the thorax and abdomen about the same length. The branchial siphon is a short wide cylinder with 6 short points around the margin. Siphons are invariably curved over, directing the aperture slightly dorsally, the ventral side of the siphon being slightly longer than the dorsal side. The atrial aperture is an oval sessile opening transversely oriented across the dorsum about halfway down the thorax. It is surrounded by a narrow band of muscles. The anal opening usually projects up across the posterior rim of the opening, and an atrial tongue of variable length from very large and forked at the tip to small and stumpy, projects from the upper rim of the aperture. The largest tongues are on the zooids that surround the common cloacal apertures and the forked tip is inserted into the rim of the aperture. Crowded tapering columnar cells project from the thoracic body wall. Fine longitudinal muscles are numerous in the parietal wall of the thorax, and strong dorsal pharyngeal muscles are present on each side of the mid-dorsal line. They fade out at the posterior end of the thorax and there is no retractor muscle. Stigmata are long and narrow at each end, and about 12 are in each of the rows — a reduction in number toward the posterior end of the branchial sac was not detected.

The abdomen is long and narrow and the gut forms a narrow vertical loop. Only a small part at the pole of the loop, involving the proximal part of the rectum, is bent ventrally. The testis, behind this small flexure of the gut, consists of 5–7 follicles arranged in a circle with their rounded bases anterior and the narrow terminal points at the posterior end of the zooid where they join the proximal end of the vas deferens. Nine coils of the vas deferens surround the testis. Larvae are not known.

REMARKS. The species is distinguished by its spicules, large zooids with long vertical gut loop, lack of a retractor muscle, large branchial siphons, restricted sessile atrial apertures, the cloacal systems and the relatively large number of vas deferens coils. *P. infundibulum* has a similar number of vas deferens coils, but the common cloacal systems are different. *P. multiforme* has similar spicules, but its colonies and colonial systems are different, and it has only a surface layer of spicules. *P. regulum* also has similar spicules but they are larger, their ray length/spicule diameter ratio is less, and the zooids have fewer vas deferens coils. *P. arafurensis* has similar spicules but fewer spicule-rays and vas deferens coils than in the present species.

Didemnum grande: Kott, 1962 from Rottnest I. (AM Y1514) was said to have a divided testis. On re-examination the testis appears to have 3 or 4 follicles surrounded by 4 coils of the vas deferens and is probably a *Polysyncraton* sp. The colonies are in vegetative phase, the cloacal cavity not present and the thoraces rudimentary vegetative ones. The spicules, to 0.06mm diameter are crowded through the thin sheet-like colony, and although they have the same number of rays, as the present species, the rays are conical rather than fusiform. The species does not appear to be the same as the present one (see also *P. oceanium* Remarks).

Polysyncraton papyrus sp. nov.
(Figs 57A, 164E)

Didemnum paradoxum: Kott, 1954: 163.

TYPE LOCALITY. Tasmania (north eastern coast, BANZARE statn 115, 128m, 26.3.31, syntypes AM Y1520).

COLONY. Syntype colonies are small circular plates to 1cm in diameter and hard and raspy to the touch. Spicules are crowded throughout, although they are especially crowded in the surface and basal test. Branchial apertures are conspicuously stellate, the openings outlined in white spicules. Common cloacal cavities are thoracic, with abdomina embedded in the basal test and thoraces crossing the cloacal cavity each in a separate test sheath. Spicules are small (to 0.038mm diameter), stellate with 9–11 conical rays in optical transverse section. The ray

length/spicule diameter ratio is 0.27, and the rays are not very pointed.

ZOOIDS. Zooids are robust, brown in preservative, with a large sessile atrial aperture and well developed anterior atrial tongue. A sharp retractor muscle extends from the posterior of the thorax. Kott (1954) found 5 testis follicles with 5 or 6 vas deferens coils around them, but these were not observed in the re-examined specimens.

Larvae are present in the syntype colonies collected in March. The larval trunk is only 0.4mm long, with 8 ectodermal ampullae along each side of the 3 antero-median adhesive organs. An otolith and an ocellus are present. The oozooid has a well formed gut, the pharynx has 4 rows of stigmata, but blastozooids are not present. The tail is wound about three-quarters of the way around the trunk.

REMARKS. The species is distinguished by its small stellate spicules crowded throughout the test, robust brown zooids with distinct atrial lips and conspicuously stellate branchial apertures. The spicules are similar to those of tropical *P. rugosum* and *P. dromide*, although neither have such conspicuously round-tipped rays. The circular cloacal systems and spicule distribution of *P. dromide* also are different. The species does resemble *P. paradoxum* Nott, 1892 from Auckland Harbour, although like *P. rugosum* a retractor muscle has not been recorded for the New Zealand species. The well defined margins of spicules around the conspicuously stellate branchial apertures occur also in *P. orbiculum* (from Western Australia) which has similar stellate spicules (although they are larger than those of the present species), the ray length/spicule diameter ratio is greater and the spicule-rays are club-shaped as well as conical. *P. rubitapum* has similar well-formed branchial siphons lined with spicules which outline the margins of the apertures and similarly shaped larvae to the present species, but its spicule rays are sharply pointed, its larval trunk is larger, and it has blastozooids.

Kott (1962) considered these specimens from Tasmania (*D. paradoxum*: Kott, 1954) conspecific with the syntypes of *P. discoides* from Rottnest I. on the basis of the similarity of colonies, size of the spicules and their arrangement in the branchial apertures. However, the syntype colonies of *P. discoides* appear to be a separate species, distinguished by globular or burr-like rather than stellate spicules as in the present species. Nevertheless, *P. discoides* does occur in Tasmania, its range overlapping the range of the present species.

Kott (1954) miscounted the larval epidermal ampullae which, on re-examination, are found to be 8 per side rather than 11. The 5 or 6 vas deferens coils which Kott (1954) reported, may also be an error, since she found them to be obscure. They were not detected at all on re-examination of the material.

Polysyncraton pedunculatum sp. nov.
(Fig. 57B,C; Pl. 6D)

Polysyncraton magnilarvum: Kott, 1972b: 178.
Polysyncraton aspiculatum: Kott, 1975: 7.
Not *Polysyncraton aspiculatum*: Kott, 1962: 301 (< *P. purou* and *P. robustum*).

TYPE LOCALITY. South Australia (Investigator Strait, statn Y5, coll. J. Watson 11.01.71, holotype MV F68818; statn X15, coll. J. Watson January 1971, paratype MV F68944).

FURTHER RECORDS. South Australia (Great Australian Bight, SAM E2639 Kott, 1975; Nuyts Archipelago, SAM E2599, E2650; Yorke Peninsula, SAM E2652, QM G302867; Flinders I., QM GH2387).

COLONY. The holotype colony is a more or less flattened, irregularly lobed, roughly fan-shaped lamella (4cm wide, 2cm thick, 5cm high) with a short thick stalk (2cm diameter, 3cm long). Most known colonies are similar, with a flattened head on a short, thick stalk although the paratype colony has several rounded heads. Colonies always are aspicular.

All specimens are of the same opaque spongy consistency, with a surface layer of zooids separated from the central test core by a sometimes extensive posterior abdominal cloacal cavity. In more mature colonies zooids are in groups of up to 30, each group anchored to the central test by a narrow connective surrounded by the primary cloacal cavity, and with shallow thoracic cloacal cavities penetrating amongst the zooids. In less developed colonies the zooids are along each side of the deep, but not posterior abdominal, circular cloacal canals that form a network in the surface. There are relatively few, but large, sessile cloacal apertures along the upper free border of the holotype. The separate lobes of the paratype colony have terminal common cloacal apertures. The groups of zooids protrude slightly from the surface, the surface test over the primary canals around them being slightly depressed.

The living colonies are said to be purple. In preservative zooids are brown at first, but they

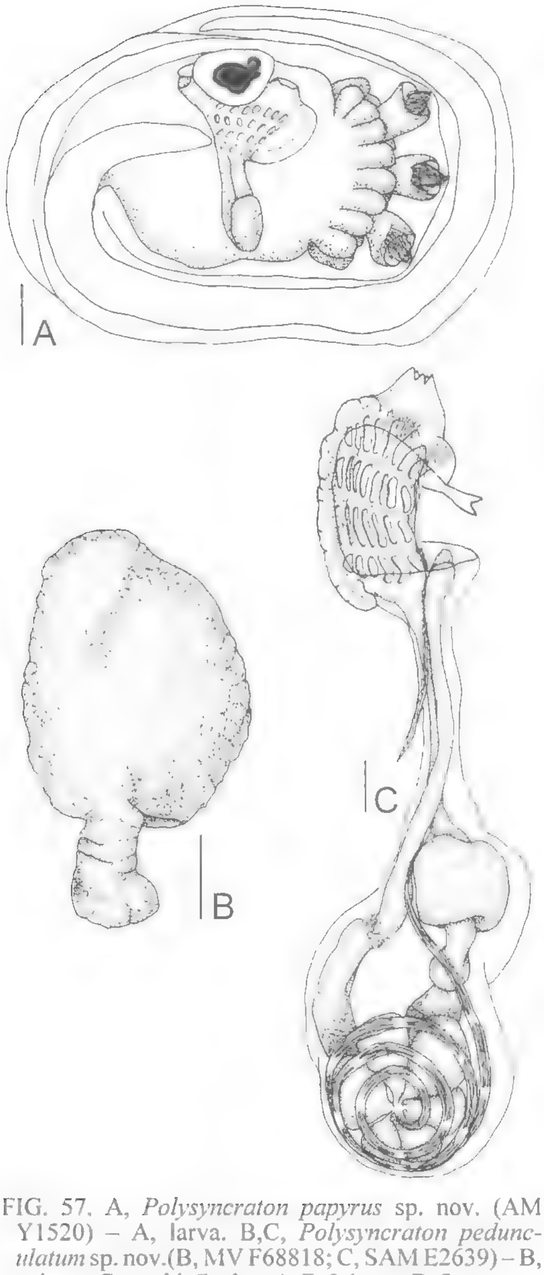


FIG. 57. A, *Polysyncraton papyrus* sp. nov. (AM Y1520) – A, larva. B,C, *Polysyncraton pedunculatum* sp. nov.(B, MV F68818; C, SAM E2639) – B, colony; C, zooid. Scales: A,C, 0.1mm; B, 2cm.

become cream and the same colour as the aspicular test.

ZOOIDS. Zooids are small, about 1mm long. The rounded tips of the projecting columnar cells are particularly crowded on the anterior part of the thorax. The branchial siphon is also long, with 6 pointed lobes. The atrial aperture is a wide opening exposing most of the dorsal half of the branchial sac. A bifid atrial tongue of varying size from the upper rim of the opening is often forked. A fine retractor muscle of variable length projects from about halfway down the relatively long oesophageal neck. The branchial sac is relatively small with about 8 stigmata in the anterior row, and 6 in the posterior row. The gut loop is short and rather rounded. Two short vascular processes project from the ventral (concave) side of the gut loop, where the proximal part of the rectum is flexed up over the gonads. Five or 6 testis follicles are dorsal to or behind the flexed part of the gut loop, with the vas deferens loosely coiled 4 times around them. Larvae are not known for the species.

REMARKS. The stalked colony is similar to *Leptoclinides fungiformis* and *L. volvus*. However, in addition to the generic differences (principally the posteriorly positioned atrial aperture), both these species have spicules and more stigmata per row. The stalked aspicular colonies, the large terminal cloacal apertures and extensive posterior abdominal primary cloacal cavities are unusual in *Polysyncraton*. The numerous male follicles distinguish the species from the New Zealand *P. chondrilla* which has similar colonies and sometimes is aspicular. *P. jugosum* also has a numerous male follicles, but never is aspicular.

Specimens from Queensland and Western Australia assigned to *P. aspiculatum* by Kott (1962) are not conspecific with the present species. The Queensland colony is *P. purou*, with similar spicules, similarly distributed; while the Western Australian specimens from Cockburn Sound although with variable spicule distribution and sometimes being aspicular, have cushion to sheet-like (rather than stalked) colonies, a horizontal thoracic cloacal cavity and more stigmata (see *P. robustum*).

Despite Kott's (1972b) proposal that *P. magnilarvum* Millar, 1962 is conspecific, it is a flat colony with relatively large stellate spicules that distinguish it from the present species.

Polysyncraton pontoniae
Monniot & Monniot, 1987
(Fig. 162H)

Polysyncraton pontoniae Monniot & Monniot, 1987: 47.

NEW RECORD. Queensland (Capricorn Group, QM G308019).

PREVIOUSLY RECORDED. French Polynesia (Monniot & Monniot, 1987).

COLONY. The newly recorded colony is thin, very soft, and breaks up readily. It was soft and orange in life. Spicules are minute and crowded throughout the test. The French Polynesian colonies, from a few mm to 5cm in greatest dimension, were yellowish to yellow-orange, marbled with white. The meandering cloacal canals (visible from the surface) always contain a pontoniid shrimp (Monniot & Monniot, 1987). Crustacean commensals were not observed in the newly recorded colony.

Spicules (to 0.08mm in diameter) are sometimes almost globular, but most are burr-like, with long, round-tipped rays, more separated from one another than in spicules usually regarded as globular. The ray length/spicule diameter ratio is about 0.4. Rays are sometimes almost cylindrical but many, including the larger ones are distinctly flattened and tongue-shaped.

ZOOIDS. Zooids are about 1mm long. The branchial siphon is of moderate length with 6 small lobes around the rim of the opening. The atrial tongue is bifid. About 8 stigmata are in the anterior rows of the branchial sac and 6 are in the posterior row. The short retractor muscle extends from the anterior part of the oesophageal neck. The gut forms an open loop with the ascending limb curved up over the gonads. Three coils of the vas deferens surround a circle of 4–7 male follicles.

Larvae are not in the newly recorded material. A not very advanced larva from the French Polynesian material (Monniot & Monniot, 1987) has a trunk 0.5mm long, the tail wound about three quarters of the distance around it, and with 4 lateral ampullae per side.

REMARKS. The tongue-shaped spicule rays of this species are unique. *P. recurvatum* (Sluiter, 1909) has a similar number of vas deferens coils, a retractor muscle, and slightly similar spicules, but its spicule rays are cylindrical, flat-tipped and more crowded and the spicules are more accurately described as globular (Kott, 1981).

Although they are distinguished by generic characters both *Lissoclinum concavum* from southern Australian waters and the New Caledonian *L. polyorchis* Monniot, 1992 have numerous male follicles and similar spicules — although in the case of the latter species they are less diverse.

Polysyncraton pseudorugosum Monniot, 1993
(Figs 58, 163H; Pl. 6E)

Polysyncraton pseudorugosum Monniot, 1993: 10.

NEW RECORDS. Queensland (Hervey Bay, QM G302185, G308347-8). Northern Territory (Darwin, AM Y2286; Bathurst I. QM G302910). Coral Sea (Murray I., QM GH253).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1993).

COLONY. Colonies are robust, leathery sheets, with the upper surface raised into rounded elevated areas separated from one another by deep, narrow depressions over circular common cloacal canals. These are lined on each side by zooids. Zooids are absent from the solid test of the elevated areas, although they are partly embedded around their perimeter. Spicules are crowded throughout the test, being absent only from a thin layer of spicule-free test that lines the floor, walls, and roof of the common cloacal canals and surrounds the zooids. The common cloacal canals are deep, extending the full length of the zooids between a thin layer of surface test and a thicker layer of basal test. Although sometimes interrupted by common cloacal canals, the colony has 3 horizontal layers of crowded spicules, of almost equal thickness, viz. the surface layer (pierced by branchial siphons), the middle layer (pierced by the oesophageal necks of the zooids), and the basal layer (beneath the zooids). Thoraces cross the cloacal cavity between surface and middle layers, and the spicule filled test is interrupted by the embedded abdomina between the basal and middle layers. The surface of the colony has evenly spaced slightly protuberant stellate branchial apertures outlined in spicules forming small pimples on the surface.

In life, the test and zooids of a colony from Hervey Bay (QM G302185) are said to have been orange rufus[R] before fading to white during long-term alcohol preservation. The colony from Bathurst I. (QM G302910) may have been the same colour, although the white spicules in the surface elevations dominate the deck photograph.

Spicules are to 0.07mm diameter with 9–11 conical rays in optical transverse section. The rays generally are sharply pointed, although in many spicules they are broken at the base. The ray-length/spicule diameter ratio is about 0.33.

ZOOIDS. Zooids are relatively large, almost 2mm long when expanded. The extended thorax (AM Y2286) is top-shaped, tapering to its posterior end. It is rounded anteriorly, the branchial aperture almost sessile in a wide, almost flat circular pre-tentacular area, the diameter of the tentacular ring being particularly wide and tending to distort the shape of the branchial siphons. In other specimens with slightly contracted thoraces the cylindrical

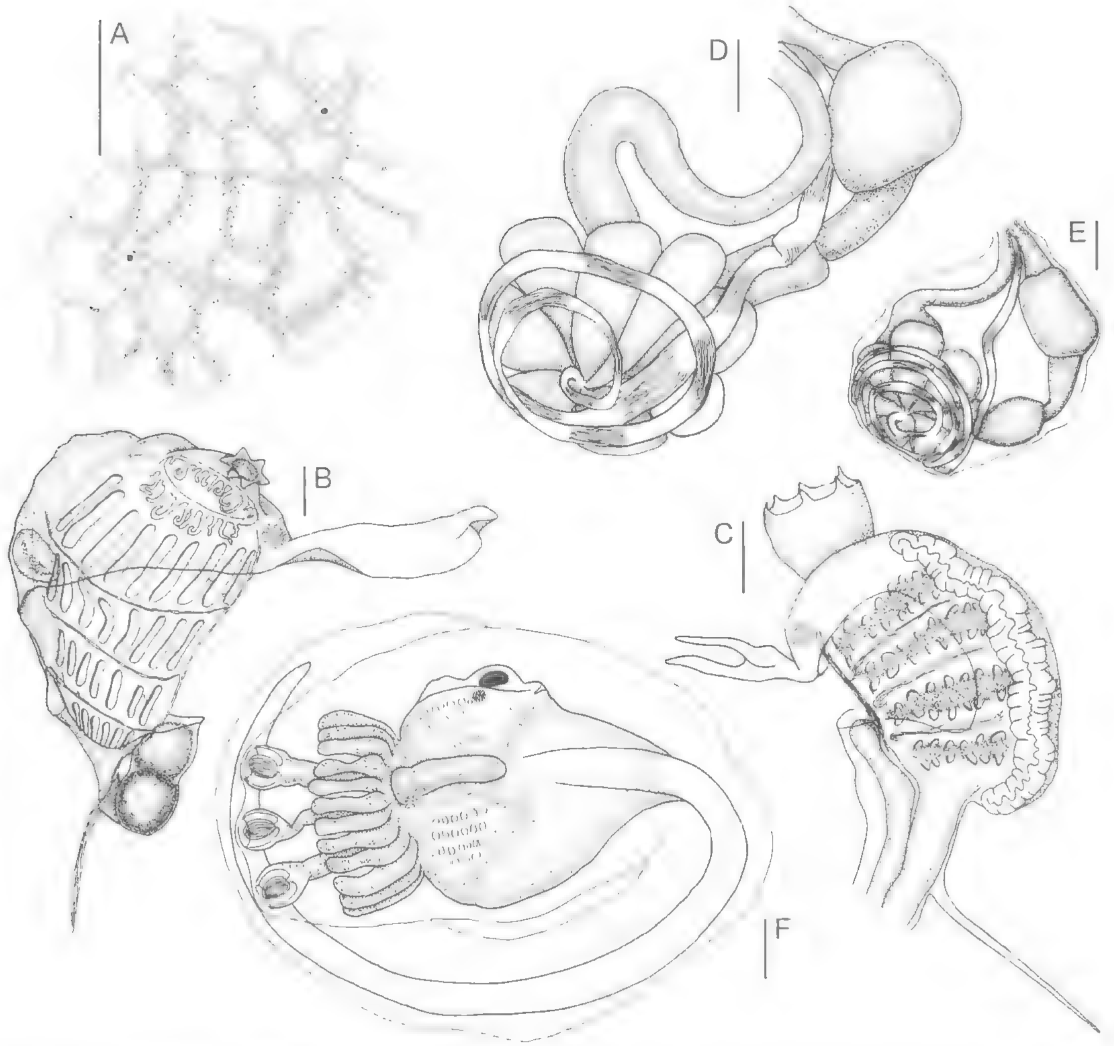


FIG. 58. *Polysyncraton pseudorugosum* (A,B,E, AM Y2286; C,D, QM 302185; F, QM G302910) – A, surface of colony; B,C, thoraces; D,E, abdomina; F, larva. Scales: A, 0.5cm; B–F, 0.1mm.

branchial siphons characterise the zooids. A long bifid atrial tongue of variable length usually projects from the anterior rim of the large atrial aperture which exposes most of the dorsal surface of the branchial sac directly to the common cloacal cavity. A conspicuous but short, tapering retractor muscle projects from the posterior end of the thorax. Nine long fusiform stigmata are in the anterior row of the branchial sac, 8 in the second, 7 in the third and 5 in the last row. The lateral organ is a shallow saucer-like concavity opposite the interspace between the first and second rows of stigmata and just ventral to the side of the atrial aperture. The oesophageal neck is relatively short, the gut loop rounded, the post-pyloric part slightly bent ventrally, and the distal part of the rectum is narrow and cylindrical as in other *Polysyncraton* spp. The gonads are on the dorsal side of the gut loop, against its ventral flexure. Seven testis follicles are surrounded by 3 loose coils of the vas deferens except in one specimen (AMY2286) from Darwin which has 4 coils.

Larvae (in specimen QM G302910 from Bathurst I.) have a corona of about 24 ectodermal ampullae around the 3 antero-median adhesive organs and on the left an external horizontal ampulla projecting back from the waist between the adhesive array and the remainder of the trunk. The cerebral vesicle has ocellus and otolith and

an oozooid and thoracic blastozooid, each with 4 rows of stigmata. The larval trunk is 0.8mm long with the tail wound two-thirds of the way around it. In the New Caledonian material (Monniot, 1993), the larval trunk is 0.75mm long and a thoracic blastozooid is present, but the 3 adhesive organs are surrounded by a circle of only 16 ectodermal ampullae (8 per side).

REMARKS. This readily characterised species is separated from *P. magnetae* (which has the same colony form) by its larger stellate spicules and position of the retractor muscle. Many characteristics of the zooids resemble *P. arafurensis*, which overlaps part of the range of the present species (in the Arafura Sea). Spicules of *P. arafurensis* have more numerous and more sharply pointed rays, its upper surface is smooth and its common cloacal cavity is a simple horizontal thoracic space, crossed by separate thoraces each associated with a ventral test sheath.

The type specimen of *P. pseudorugosum* Monniot, 1993 from New Caledonia has a similar colony, zooids and spicules to the newly recorded material, although the larvae from Bathurst I. have more ectodermal ampullae than the New Caledonian ones, which have only a total of 16. The species is distinguished from *P. millepore* by its orange colour, fewer vas deferens coils and lack of spicules with short, truncated rays.

Polynsyncraton pulchrum sp. nov.
(Figs 59, 162A)

TYPE LOCALITY. Western Australia (Cockburn Sound, coll. Marine Sciences Camp 17-21.5.71, holoytpe WAM 137.93; SW Woodman's Point, 18m grey mud, coll. L. Marsh and S.M. Slacksmith 20.2.91, paratype WAM 176.91).

FURTHER RECORDS. Western Australia (Cockburn Sound, WAM 6.95, QM G9672).

COLONY. Colonies are flaccid, soft, upright, flattened (holotype) or almost spherical (paratype) lobes to 3cm high and 4cm long. Two large, open, common cloacal apertures are each on a slight prominence, one at each end of the upper surface of the laterally flattened holotype. The paratype has a single, large, terminal cloacal aperture. Branchial apertures are evenly spaced over the surface, with spicules in a layer in the siphonal linings which, when seen from the surface appear as a margin of spicules outlining the stellate openings. Spicules are slightly less crowded immediately around each branchial aperture than they are between the zooids — where they form an opaque white meshwork evident from the surface of the colony. There is no superficial layer of bladder cells. Spicules are sparse in the internal test of the colony. They are all burr-like to 0.05mm diameter, with up to 21 long, crowded, rod-like rays with flat or irregular tips, or fusiform ones narrowing at each end. Large posterior abdominal cloacal spaces separate the outer zooid-bearing layer from the central test mass, and these spaces are continuous with those that extend the whole length of the zooids to separate clumps of zooids from one another.

Colonies are white in preservative. Their living colour is not recorded.

ZOOIDS. Zooids are about 2.5mm long when the thorax is contracted, but may be nearly 3mm when relaxed. The branchial aperture is short, with 6 shallow lobes, and the atrial aperture is a wide, sessile, transverse opening across the posterior third of the dorsal surface of the thorax. Lateral organs were not seen. Stigmata are in 4 rows of about 12. The post-pyloric part of the gut loop is long, with its posterior or distal part slightly kinked ventrally. Gonads lie against the dorsal surface of the distal part of the loop. The stomach is vertical and egg-shaped, the duodenum long, and the oval posterior stomach is in the descending limb of the loop. The testis consists of 7–9 long club-shaped follicles. Six to 8 of these are arranged in an outer ring around one or 2 central follicles. The testis follicles converge to the postero-dorsal point of the zooid where they join the vas deferens, which makes only 4 turns around the testis. A large egg is to the right of, slightly posterior to the testis and within the 2 outside coils of the vas deferens.

REMARKS. Although an extensive posterior abdominal cavity is present, absence of an atrial siphon, loose coils of the vas deferens and position of the ovary inside its outer coils, indicate an affinity with *Polysyncraton* rather than *Leptoclinides* despite the posterior position of the atrial opening and the extensive posterior abdominal cloacal cavity.

The species resembles *P. circulum*, but it lacks surface vesicles and has distinctive soft colonies and posterior abdominal cloacal cavities. The soft flaccid colonies, consisting of relatively few systems, resemble those of some *Didemnum molle*.

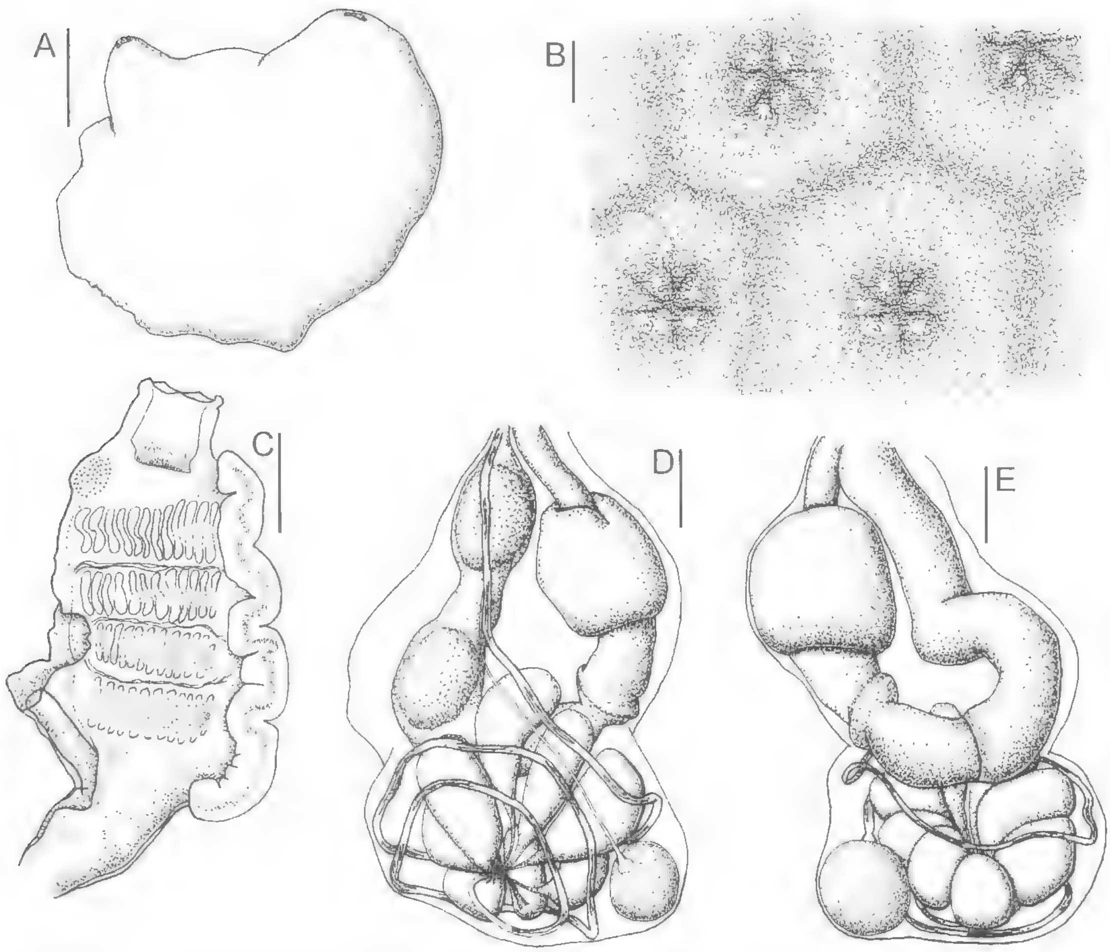


FIG. 59. *Polysyncraton pulchrum* sp. nov. (WAM 137.93) – A, outline of colony; B, colony surface showing branchial apertures; C, thorax; D, abdomen dorsal view; E, abdomen ventral view. Scales: A, 1.0mm; B–E, 0.2mm.

Polysyncraton purou
Monniot & Monniot, 1987
(Figs 60, 162C; Pl. 6F)

Polysyncraton purou Monniot & Monniot, 1987: 49.
Polysyncraton aspiculatum: Kott, 1962: 301 (part, colony from Mackay).

NEW RECORDS. Queensland (Heron I., QM G301515, G301559, G302951, G302999, G308050, G308121-2 G308230-1, G308275; Lizard I., QM G301574, AM Y2323).

PREVIOUSLY RECORDED. Queensland (Mackay – AM Y1488 Kott, 1962). French Polynesia (Monniot & Monniot, 1987).

COLONY. Colonies are firm (but not tough), gelatinous and translucent with a (usually) discontinous layer of spicules, the spicules being in irregular patches or clouds or long strips, beneath a thick superficial layer of bladder cells mixed with pigment cells. In one colony this layer of spicules beneath the bladder cell layer is not interrupted. Spicules are especially crowded over the anterior ends of each zooid where the surface of the colony sometimes is raised into small elevations. Spicules are not present elsewhere. Branchial apertures are conspicuous, with 6 small groups of spicules in the siphonal linings. Common cloacal apertures are in clear lens-shaped spicule-free areas of test. Common cloacal canals are thoracic with zooids arranged along each side of them. The surface often is depressed over the cloacal canals, which appear to surround elevated areas of zooid-free test. Spicules are stellate, to 0.07mm in diameter with 13–15 long crowded rays in optical transverse section. The rays are either pointed and almost

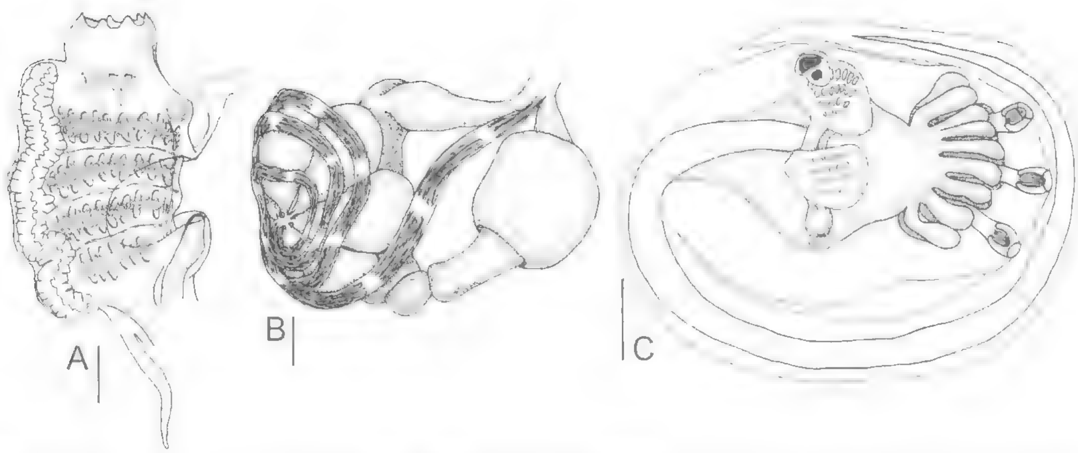


FIG. 60. *Polysyncraton purou* (A, B, QM G308230; C, QM G302951) – A, thorax; B, abdomen; C, larva. Scales: A, B, 0.1mm; C, 0.2mm.

fusiform or some are blunt- or flat-tipped or club-shaped. The spicules break up very readily.

Overall, living colonies are flesh colour[R], or orange or orange-chrome[R], or orpiment orange[R], or scarlet vermilion[R] or slate black[R], with dark brown[R], ferruginous[R], chinese orange[R] or burnt carmine[R] coloured zooids. The colonies become pale orange to white in preservative. *Prochloron* is in patches on the surface. Sometimes the preservative is stained yellow-orange.

ZOOIDS. Relaxed zooids are relatively large, being 2mm long overall. The thoracic and abdominal body wall are covered with fine projecting columnar cells. The branchial aperture has 6 shallow points. The atrial aperture is large and most of the branchial sac is exposed directly to the cloacal cavity. A long atrial tongue, forked at the tip, projects from the anterior rim of the opening. The parietal body wall has fine longitudinal muscles and an almost spherical flask-like lateral organ with the opening directed ventrally is invaginated into it. A long, fine retractor muscle projects from the upper part of the oesophageal neck. The branchial sac has about 10 stigmata in the anterior row and 8 in the middle rows. The gut loop is long with the usual subdivisions, and the proximal part of the ascending limb is looped up over the gonads. The testis has 5–8 pear-shaped male follicles arranged in a circle, and surrounded, usually, by 3 (QM G302951) but occasionally by 2 (QM G308050) or 4 (QM G308230) vas deferens coils.

Larvae are in colonies collected in March (QM G308050) and October (QM G302951) from Heron I. The larval trunk is about 1mm long, and the tail winds almost the whole way around it. The single larval blastozooid has 4 rows of stigmata, and 4 rows are in the oozooid. The 8 or 9 lateral ampullae on each side arise by subdivision of primary ones. In one of the larvae, the axillary cone of one of the adhesive organs has subdivided, and in others there are 4 rather than the usual 3 adhesive organs. An external lateral ampulla projects from the larval epidermis on the left side.

REMARKS. Characteristics of the species are its fleshy colonies with a single layer of spicules beneath a thick superficial bladder cell layer and its robust zooids with a large atrial tongue and fine retractor muscle.

The newly recorded material has zooids, colony and spicules similar to the type material from French Polynesia (Monniot & Monniot, 1987) in most respects although the zooids and the larval trunk of the latter are smaller than those from Heron I.

P. aspiculatum: Kott, 1962 from Mackay (AM Y1488) is not conspecific with the South Australian *P. magnilarvum*: Kott, 1972b (<*P. robustum*) and *P. aspiculatum*: Kott, 1975 (< *P. pedunculatum*) as Kott (1975) proposed. The specimen from Mackay appears to be *P. purou* forming a flat and investing colony (rather than a stalked one like *P. pedunculatum*). It has spicules beneath a superficial layer of bladder cells in the vicinity of thoracic common cloacal canals with zooids arranged along each side of them. Spherical, brown pigment cells are present in the surface test, especially over the cloacal canals and the zooids are large, with a long bifid atrial tongue, up to 8 male follicles and 4 coils of the vas

deferens. The specimens from Rottnest I. (also assigned to *P. aspiculatum*: Kott, 1962) appear to be a different species which, although it has similar spicules and the same number of larval lateral ampullae as the present one, has a larger larval trunk, more coils of the vas deferens, an open, horizontal cloacal cavity, and more variation in distribution of the spicules .

Spicules of the present species slightly resemble those of *Didemnum chartaceum*, but have fewer rays. *P. multiforme* has similar spicules, but lacks the thick bladder cell layer on the upper surface. Colonies of the present species are very like *P. meandratum* with the single interrupted layer of spicules beneath the surface layer of bladder cells. However, the present species has larger stellate spicules with fewer rays (unlike the globular ones of *P. meandratum*), less muscular thoraces and is orange or orange-chrome[R] rather than brown. Generally the zooids are similar in both species, though there are fewer coils of the vas deferens and more male follicles in newly recorded specimens of the present species than in *P. meandratum*. *P. otuetue* Monniot & Monniot, 1987 is another similar species, although it has distinctly stellate spicules with relatively short conical rays. Colonies of the present species often are the same shade of orange as *P. circulum*, but they are generally fleshy, translucent and gelatinous, with bladder cells on the surface, while those of *P. circulum* are opaque with a hard continuous superficial layer of spicules. *P. dromide* has similar large larvae with blastozooids, 8 pairs of lateral ampullae, circular cloacal canals and spicules confined to the region around the common cloacal canals. However, it has much smaller (to 0.03mm diameter) and more diverse (including burr-like) spicules.

Polysyncraton regulum sp. nov.
(Figs 61A–D, 163C)

TYPE LOCALITY. Queensland (Hervey Bay rubble fauna, coll G. McKoen 1966, holotype QM G308474).

FURTHER RECORDS. Queensland (? Heron I. 8-9m, QM G302266).

COLONY. The preserved colony is a thin, irregular sheet. Large (to 0.1mm diameter) spicules are present throughout and especially crowded in the surface test. Spicules line the branchial siphon and outline the margin of the stellate apertures. A spicule free area surrounds each aperture and is seen as a circle of 6 naked spots around the aperture. Spicules have 13–15 conical, pointed rays in optical transverse section. The ray length/spicule diameter ratio is 0.25.

The common cloacal cavity is thoracic, each thorax crossing it with a ventral strip of test. Abdomina are embedded in the basal test, where translucent yellow embryos are being incubated and some tailed larvae were found. The colour of the living colonies has not been recorded.

ZOOIDS. Zooids are robust, about 1mm long with thoraces contracted. Six rounded lobes surround the branchial aperture. The atrial aperture is a wide opening with a large, muscular anterior lip with a bifid tip. The dorsal pharyngeal muscles are conspicuous and contracted, and the retractor muscle, projecting from the upper part of the oesophageal neck, is of various lengths, from short and thick to long, fine and tapering. The branchial sac has about 8 stigmata in each of the 4 rows although these could not be counted accurately. A conspicuous lateral organ projects from each side of the thorax. The vertical gut loop has the usual divisions, and in the single available colony the abdomen is dominated by a large yellow egg. The vas deferens may have 2 spirals around the testis, but the ovum often diverts the outer coil of the vas deferens around it, and distorts the remaining coil into a hook over the outside of the testis. The testis is flattened by the large egg, and sometimes only one or 2 male follicles (of a maximum of 3) were detected.

Embryos (including larvae) in the basal test are relatively small. The larval trunk is 0.5mm long and the tail is wound about two-thirds to three quarters of the way around it. Four primary ectodermal ampullae along each side of the 3 antero-median adhesive organs are each subdivided to form a total of 16 around the anterior end of the trunk. An ocellus and an otolith are present, but adult organs are not well developed. Some stigmata are developing in the pharyngeal wall, but the exact number of rows was not determined. the trunk. Two rudimentary blastozooids are present.

The specimen from Heron I. questionably assigned to this species has identical spicules to the type specimen, but zooids were not detected.

REMARKS. Although the testis is underdeveloped and flattened, and the number of small lobes present is not always clear, this specimen exhibits many *Polysyncraton* characters, and its generic assignation is not in doubt. A particularly well developed muscular atrial tongue, relatively few and loose coils of the vas deferens and larvae with many ectodermal ampullae, blastozooids,

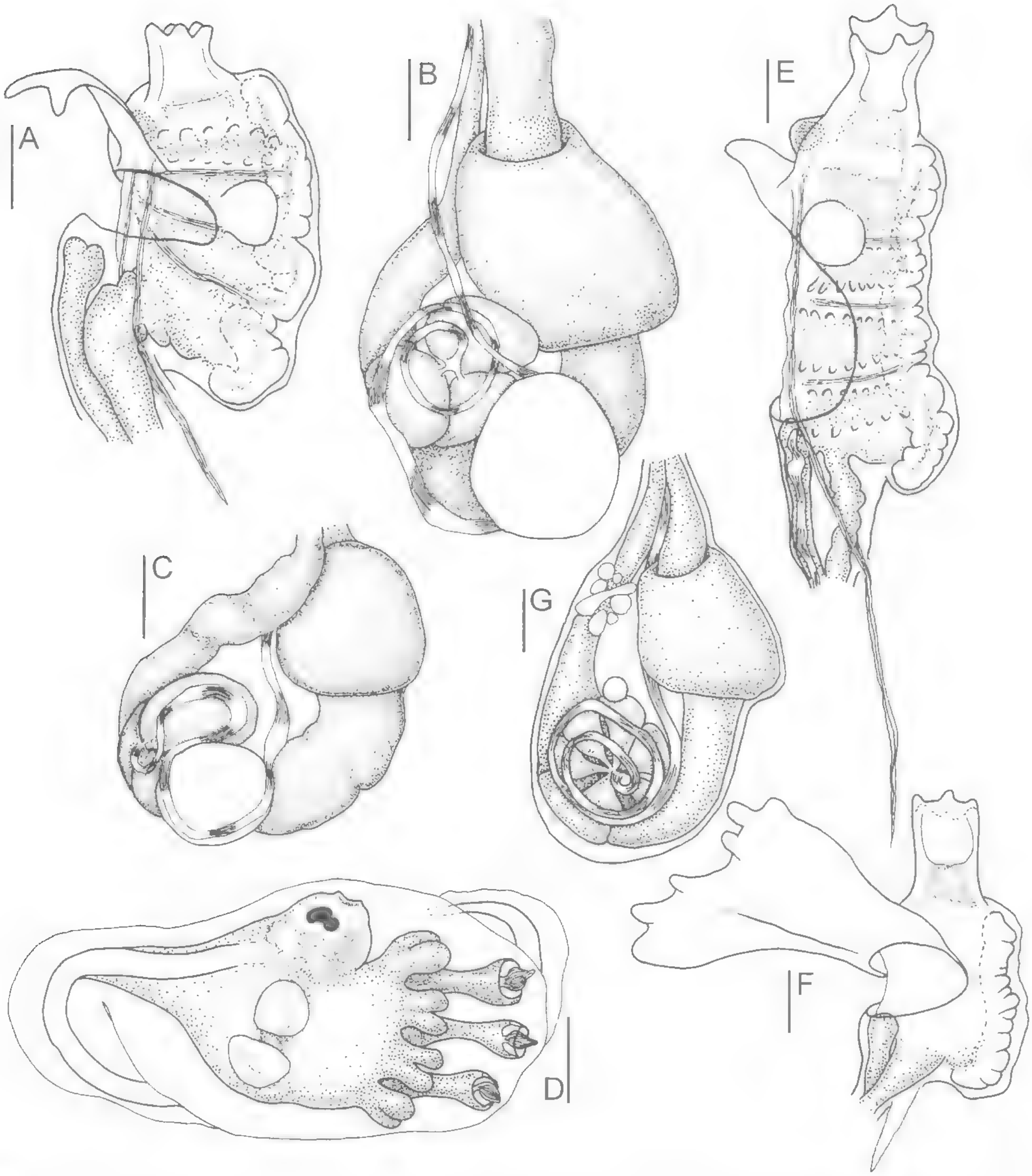


FIG. 61. A – D, *Polysyncraton regulum* sp. nov. (QM G308474) – A, thorax; B, abdomen; C, abdomen, coils of vas deferens disturbed by developing egg; D, larva. E – G, *Polysyncraton rica* sp. nov. (QM GH5426) – E, thorax; F, thorax with well developed atrial tongue; G, abdomen. Scales: 0.1mm.

underdeveloped adult organs and attenuated posterior end of the larval trunk are characters generally occurring together in this genus. The species is similar to *P. arafurensis*, with a similar number of vas deferens coils, and a retractor muscle. However, in the present species the spicules are larger. *P. pseudorugosum* has a similar larva but 3 coils of the vas deferens, smaller spicules with fewer and not such sharply pointed rays, and distinctive surface sculpture on the colony. Although *P. rugosum* has a similar number of larval ectodermal ampullae and a similar number of vas deferens coils which are diverted by the development of the ovum, it has

different and smaller spicules and lacks the conspicuous retractor muscle of the present species.

Polysyncraton rica sp. nov.
(Figs 61E,F, 165C; Pl. 6G)

TYPE LOCALITY. South Australia (Kangaroo I., D'Estrées Bay, 6m, seagrass bed, coll. AIMS Bioactivity Group 25.1.89, holotype QM GH5426; paratypes QM G308487).

COLONY. Colonies are fleshy cushions to 1cm thick. Beneath a conspicuous, smooth, superficial bladder cell layer spicules are crowded in the zooid bearing layer of the colony which is almost completely separated from the fleshy basal two-thirds (in which spicules are increasingly sparse). Zooids are in large clumps, surrounded by deep primary canals and anchored to the basal test by a stout central connective that interrupts a horizontal posterior abdominal common cloacal cavity. Secondary cloacal spaces penetrate amongst the thoraces.

The upper surface of the colony is elevated into rounded swellings with terminal common cloacal apertures but these are inconspicuous in the preserved material. Branchial apertures also are inconspicuous, evident only from the plug of spicules in each. The spicules are stellate, but not always spherical, some being irregular with one axis longer than the other. The longest axis is up to 0.07mm, and the spherical spicules are up to 0.07mm diameter. They have robust conical rays, sometimes with flattened sides to form pyramids with sharp edges. The rays, 11–13 in optical transverse section, are pointed or chisel-shaped and often are bifid or the whole ray appears to be divided. The ray length/ spicule diameter ratio is up to 0.33.

In life, the colony is pink with a transparent veil, created by the colourless bladder cell layer that over lies the pink colour of the zooid layers.

ZOOIDS. Zooids are relatively large with a long thorax to about 0.8mm and abdomina about 0.6mm long. A fine long retractor muscle projects from the upper part of a short oesophageal neck. The branchial siphon is short and cylindrical with 6 pointed lobes around the apertures. The atrial aperture is a large more or less circular, sessile opening wrapped around the dorsum of the branchial sac. A large, but variable atrial tongue projects from the anterior rim of the opening. It sometimes is particularly broad, wider along its curved distal edge which sometimes has about 5 short, pointed, fringing processes. A circular saucer-shaped, lateral organ is depressed into the parietal body wall opposite the first row of stigmata — at the antero-lateral corner of the atrial aperture. Stigmata were not accurately counted. The relatively short compact abdomen has a simple vertical gut loop divided into stomach, long duodenum, short posterior stomach and broad rectum. The testis, against the dorsum of the distal part of the gut loop, consists of 6 or 7 follicles, and the vas deferens coils 3 times. Larvae are not known.

REMARKS. The sympatric *P. tegulum* has similar zooids with long thoraces and atrial tongues, similar but larger and more regular stellate spicules, more (7) coils of the vas deferens, thinner colonies with spicules throughout and there is no posterior abdominal cloacal cavity. *P. pedunculatum* and the central NSW species *P. jugosum* also have a posterior abdominal cloacal cavity (an unusual character in this genus) but have other characters distinguishing them.

Polysyncraton robustum sp. nov.
(Figs 62, 163A)

Polysyncraton aspiculatum: Kott, 1962: 301 (part, specimens from Western Australia).

TYPE LOCALITY. Western Australia (Point Peron west of Point John, sides and undercut of sheltered pools, coll. P. Kott December 1948, holotype AM Y2315; Rottnest I., Salmon Bay, inner pool, coll. P. Kott 18.11.51, paratypes AM Y2313-4).

FURTHER RECORDS. Western Australia (Rottnest Island, Salmon Point, AM Y2312).

COLONY. Colonies are fleshy, gelatinous sheets to about 4cm in maximum dimension. The superficial bladder cell layer is thin, although it is thicker around the margin of the colony. Abdomina are embedded in the basal test, and the common cloacal cavity is extensive and horizontal with thoraces crossing it in their own sheath of test.

Spicule distribution is variable, sometimes aspicular (AM Y2314), with spicules moderately crowded to sparse beneath the bladder cell layer, and less crowded beneath the thoracic common cloacal cavity (AM Y2313), or present, but sparse throughout, becoming more sparse toward the base (AM Y2312). In the holotype they are sparse in the basal layer of test (beneath the cloacal cavities) but a thin layer is on the base of the colony, and occasionally some patches occur at thoracic level around the outer margins of the colony. Spicules are to 0.06mm diameter with about 15–19 long, more or less pointed or flat- to round-tipped rays in optical transverse

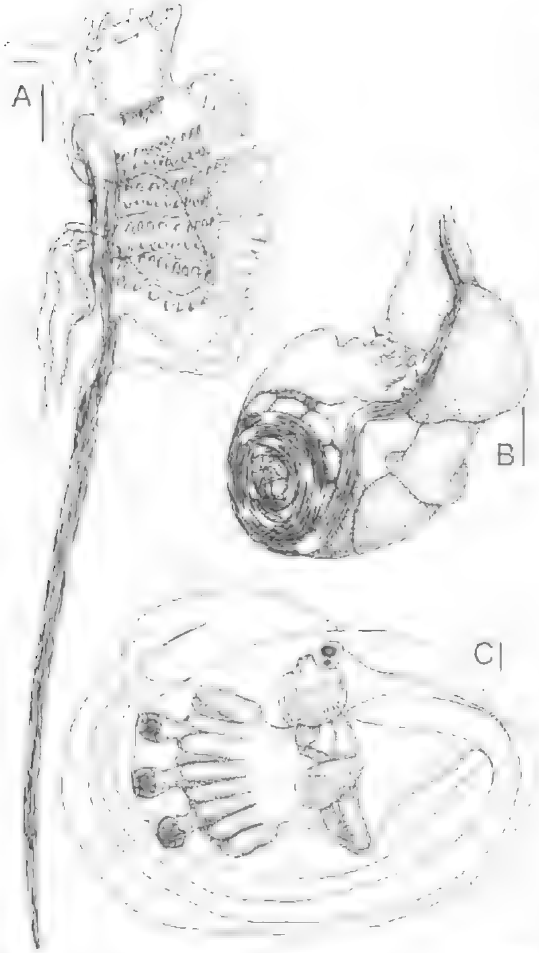


FIG. 62. *Polysyncraton robustum* sp. nov. (AM Y2314) – A, thorax; B, gut loop and testis; C, larva. Scales: 0.1mm.

section. When spicules are present in the surface test they project down into the siphon linings in 3 radial, paired rows.

ZOOIDS. Zooids are relatively large with a moderately long branchial siphon and a long, bifid atrial tongue from the anterior rim of the large opening. A long, fine tapering retractor muscle projects from the posterior end of the thorax. Twelve stigmata are in the anterior row, and reduce to 8 in the posterior row. The testis is divided into 8–12 follicles surrounded by 5 loose vas deferens coils.

Larvae in all the Western Australian material (collected in November and December) have a 1.4–1.7mm long trunk with 8 ectodermal ampullae along each side of the 3 anterior adhesive organs. Kott's (1962) account of 11 pairs of lateral ampullae in these larvae could not be confirmed. An oozooid and abdominal and thoracic buds of a blastozooid are about halfway along the trunk. A large ocellus and otolith are in the cerebral vesicle of the oozooid.

REMARKS. These specimens differ from the Japanese *P. aspiculatum* Tokioka, 1949a (to which they were assigned originally) in the presence of spicules and larval blastozooids. *P. magnilarvum* Millar, 1962 from South Africa has more larval ectodermal ampullae and its zooids are not in circular systems although its larval trunk and its spicules are a similar size to the present species.

P. aspiculatum: Kott, 1975 (<*P. pedunculatum*) from the Great Australian Bight is a different aspicular, soft, gelatinous, stalked species with fewer stigmata in the branchial sac.

Tropical *P. purou* probably resembles the present species most closely and formerly was confused with it. Like the present species it has a jelly-like consistency, restricted spicule distribution and similar spicules, zooids and larvae. However, *P. purou* has smaller larvae, and its common cloacal cavity is more restricted than the large horizontal spaces of the present species.

Polysyncraton rubitapum sp. nov.
(Figs 63, 165A)

TYPE LOCALITY. South Australia (Top Gallant I. 5m, coll. S. Shepherd et al., 29.3.81, holotype QM GH1330).

COLONY. The colony is a hard, irregular, encrusting sheet with the surface depressed slightly over the common cloacal canals which have zooids along each side and surround slightly protuberant circular areas of zooid-free test. The solid basal test is up to 3mm thick, and the thoracic cloacal cavity and the surface test are, together, about 5mm thick.

Uniform stellate spicules to 0.05mm diameter, with 7–9 sharply pointed conical rays in optical transverse section occur throughout the colony and line the margins of the stellate branchial apertures. The ray length/spicule diameter ratio is 0.3.

The living colony is said to have been red.

ZOOIDS. Zooids are large and robust, and the thorax is almost rectangular. It has a short branchial siphon with pointed lobes on the rim of the aperture, and large spherical lateral organs near the anterior end of the atrial aperture. The atrial aperture is large and sessile with a relatively short, sometimes forked lip from the anterior rim of the opening. A retractor muscle was not

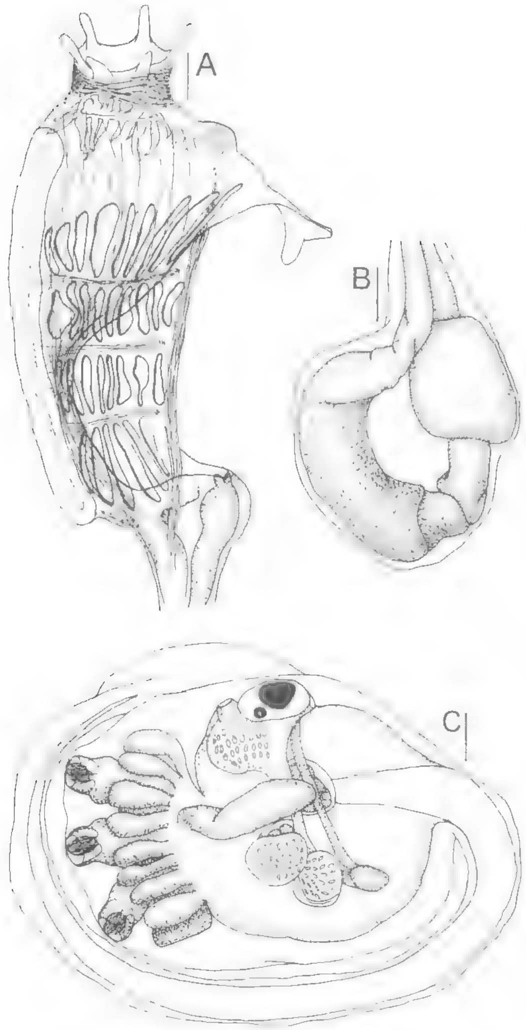


FIG. 63. *Polysyncraton rubitapum* sp. nov. (QM GH1330) – A, thorax; B, gut loop; C, larva showing blastozooids. Scales: 0.1mm.

detected. Round-tipped columnar cells were detected projecting from the posterior wall of the thorax. Nine long, fusiform stigmata are in the anterior row, and reduce to 6 in the posterior row. Gonads were not detected in the holotype, although embryos were found being incubated in the basal test.

The larval trunk is large (about 0.85mm long and relatively deep) and the tail is wound about three quarters of the way around it. Three relatively large antero-median adhesive organs have thick cylindrical stalks and are surrounded by 8 crowded lateral ampullae (resulting from the subdivision of the primary 4) on each side. On the left side of the trunk a long, thick balloon-like horizontal external lateral ampulla projects from the larval epidermis from just behind the frontal lobe with its adhesive array. It extends posteriorly to about halfway along the trunk. A large ocellus and otolith are in the cerebral vesicle and 2 blastozooids with both thoracic and abdominal buds are in the well advanced larva.

REMARKS. Although gonads are not developed the species is assigned to *Polysyncraton* on the basis of large zooids with an atrial tongue and without a retractor muscle, and the large larvae with numerous lateral ampullae, large external lateral ampulla, blastozooids, and 4 rows of stigmata. Some of these characters occur in *Didemnum* spp. (*D. chartaceum* etc.) However, absence of a retractor muscle and the 4 rows of stigmata in the larva are, with the other characters, indicative of *Polysyncraton*. Species characters are moderate-sized stellate spicules with relatively few rays crowded throughout, absence of a bladder cell layer and restricted cloacal spaces with some zooid-free areas of test.

Of other temperate species in the genus, *P. sideris* has similar but much larger spicules, and *P. orbiculum*. has spicules with blunter rays, although they are a similar size to those of the present species. Both *P. sideris* and *P. orbiculum* have large vesicles in the superficial test which interrupt the spicules and distinguish them from the present species.

Polysyncraton rugosum Monniot, 1993
(Figs 64, 162G; Pl. 6H)

Polysyncraton rugosum Monniot, 1993: 12.

NEW RECORDS. Queensland (Swain Reefs, QM G305554).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1993).

COLONY. In life the newly recorded colony is a slab about 5mm thick, spotted, with maroon pigment patches about 1.0cm apart on the surface and chrome-yellow zooids. In preservative the pigment patches in the surface test become black and the rest of the colony is white with colourless zooids. The pigment is in irregular branched, as well as spherical, cells in the thin superficial layer of test. Neither common cloacal apertures nor cavities were detected in this specimen. The type material from New Caledonia was reported to be rose-orange or maroon and the surface, rough and to have elevated cloacal apertures on short chimneys (Monniot, 1993).

Spicules, crowded throughout the colony, are small (to 0.03mm diameter), burr-like with rod-like, blunt-tipped, or chisel-shaped and loose, rather than compact, rays.

ZOOIDS. Zooids are about 1.5mm long. The branchial siphon is short with 6 shallow branchial lobes. The large atrial aperture, exposing most of the branchial sac, has a long atrial tongue with a slightly bifid tip from the upper rim of the aperture. A retractor muscle was not detected. About 8 short but fusiform stigmata are in the anterior row of the branchial sac. The gut has the usual subdivisions of rounded stomach, long duodenum, broad mid-gut, wide proximal and narrow distal parts of the rectum. Sometimes it is an almost vertical loop but in other zooids the distal part is bent up against the proximal pyloric part, with the well-developed testis behind the flexed part of the loop. Seven long male follicles are arranged in a circle surrounded by 3 loose coils of the vas deferens. The testes are mature in the newly recorded specimen. Large larvae, with a larval trunk 1.1mm long with 12 lateral ampullae per side, 3 median adhesive organs and a single blastozooid are in the type. Larvae were not in the Swain Reefs colony (collected in July).

REMARKS. The newly recorded material has the same zooids and spicules as the New Caledonian type. The absence of cloacal cavities in the present colony suggests that the colony (which has mature male gonads) may be regressed. Spicules most resemble those of *P. discoides* in which, as in the present species, a retractor muscle has not been detected. The tropical range and pigmented surface test of the present specimen are the only reliable means of distinguishing it from *P. discoides*. The larva of *P. discoides* is not yet known. The small burr-like spicules are about the same size as those of *P. dromide*, but they lack the occasional pointed rays of the latter species. The spicules of *P. purou* have predominantly pointed rays. *Polysyncraton meandratum* has similar but larger spicules and they are not crowded throughout the colony.

The species resembles *P. paradoxum* Nott, 1892 (from Auckland harbour) in its small crowded burr-like spicules, the absence of a retractor muscle and the 7 male follicles. The 3 coils of the vas deferens in the present species rather than the 4 reported in *P. paradoxum* may not represent a significant difference, and the specimens may be conspecific — other tropical species possibly occur in Auckland Harbour (see *P. meandratum*).

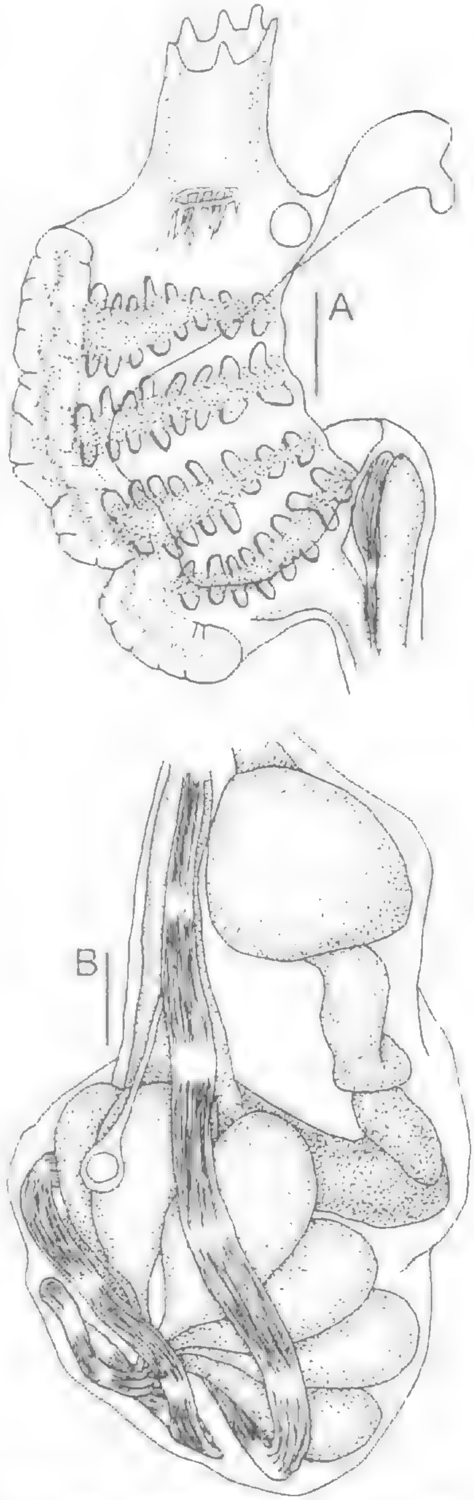


FIG. 64. *Polysyncraton rugosum* (QM G305554) – A, thorax; B, abdomen. Scales: 0.1mm.

Polysyncraton scobinum sp. nov.
(Figs 65, 164B)

TYPE LOCALITY. Queensland (Wistari Reef, boat landing, low tide rubble fauna, coll. P.Kott et al., 07.03.93, holotype QM G308049; 15m, coll. J.Kennedy 11.09.93, paratype QM G308179).

FURTHER RECORDS. Queensland (Heron I., QM G308167, G308170, G308214, G308257, G308332, G308479).

COLONY. Colonies are hard and irregular, with rounded margins. They are found growing around and between irregularities in hard substrates, and are difficult to remove. Large (to 0.14mm diameter) spicules are crowded in the surface test making it raspy to the touch. Spicules are sparse between surface and basal test except where solid zooid-free spicule-filled columns of test project vertically through the colony. Ventral surfaces of the thoraces are embedded in these columns of test, but other zooids crossing the cloacal cavity have only sparse spicules in the separate strip of test along the ventrum of each thorax. Abdomina are embedded in the basal test which contains only sparse spicules, and is fibrous and tough, zooids not being readily removed from it. Thickness of the surface layer of spicules, and diameter of the spicule-filled columns projecting down into the colony are variable. Spicules are in a fine layer on the base of the colony. The majority of spicules have moderately long, conical, moderately pointed, or blunt or round-tipped rays, 11–13 in optical transverse section.

In life, colonies are said to be pinkish-buff[R] (QM G308170) or straw-yellow[R] (QM G308049) or cream[R], or to have ferruginous[R] pigment scattered over the surface, especially around the cloacal apertures (QM G308214, G308479). Sometimes burnt sienna[R] zooids show throught the white surface spicules (QM G308167). In preservative the colonies are at first apricot with bright orange zooids. Later they become white. Some have *Prochloron* on the hard, smooth surface.

ZOOIDS. Zooids are about 1mm long. The length of the cylindrical branchial siphon varies with the thickness of the surface layer of spicules. The atrial aperture has an atrial tongue, bifid at the tip, and sometimes very long but often contracted up against the pharynx. Long tapering columnar cells were detected projecting from the anterior part of the thorax. A large circular lateral organ is each side of the anterior part of the thorax. Stigmata are short but fusiform, pointed at their anterior and posterior extremities. They number 9 in the anterior row, 8 in the second row,

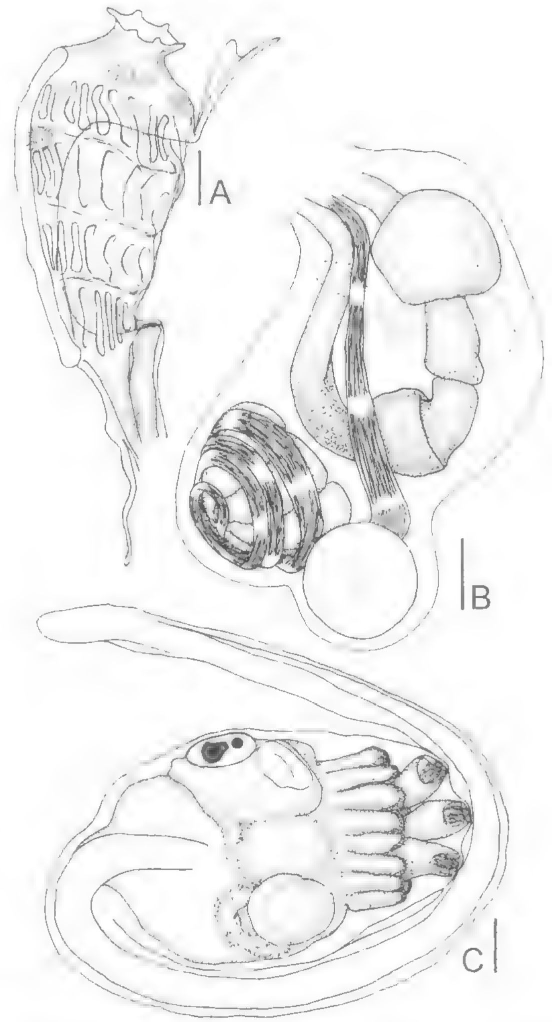


FIG. 65. *Polysyncraton scobinum* sp. nov. (A,C, QM G308332; B, QM G308049) – A, thorax; B, abdomen; C, larva. Scales: 0.1mm.

7 in the third and 6 in the posterior row. A short retractor muscle projects from the upper part of the oesophageal neck. The gut forms a wide open loop with the usual subdivisions including the long cylindrical distal part of the rectum. Four or 5 relatively short club-shaped male follicles have 5 coils of the vas deferens around them. As in many species of *Polysyncraton* the outer coil of the vas deferens passes around the outside of the ovary. Both holotype and paratype colonies are in an active vegetative phase, with parental thoraces regressing, and juvenile thoraces joined to mature abdomina. Abdominal buds were not observed.

Larvae are present in colonies collected in March (holotype: QM G308049) and October (QM G308332). The larval trunk is 0.75mm long with the tail wound about three quarters of the way around it. Eight lateral ampullae are on each side of the 3 median adhesive organs. The trunk is deep and a larval blastozooid is developing.

REMARKS. These very thin colonies with smooth hard surfaces growing around and penetrating irregularities and concavities in the substrate, large, crowded stellate spicules in the surface making it raspy to the touch, tough fibrous test around the zooids in the spicule free areas, and some vertical spicule-filled pillars of solid test are characteristic of the species.

Spicules resemble those of *P. pavimentum* Monniot, 1993 in both size and form. However *P. pavimentum* is distinguished by its discrete cloacal systems, each with a central cloacal aperture, isolated from adjacent systems, and its more numerous coils of the vas deferens (about 6). *Polysyncraton pseudorugosum*, with similar although smaller spicules with fewer rays, and a similar though slightly larger larva than the present species, has larger zooids, spicules distributed fairly evenly throughout the test and only 3 coils of the vas deferens.

Polysyncraton scorteum sp. nov.
(Figs 66, 161-I)

TYPE LOCALITY. South Australia (Great Australian Bight, Fowler's Bay jetty piles 4-5m, coll. K.L. Gowlett Holmes, W. Zeidler, B. McHenry 2.3.93, holotype SAM E2629).

COLONY. The colony is a tough leathery sheet with spicules crowded throughout. Branchial apertures on the surface are conspicuously stellate, with spicules crowded in the siphonal linings. A few large, frilled common cloacal apertures are randomly distributed over the surface. The large, open common cloacal cavity is horizontal and thoracic. Spicules to 0.07mm diameter are globular and burr-like with rounded or short conical, pointed tips on the crowded rays.

ZOOIDS. Zooids are relatively large and robust. Branchial siphons are short, wide, and muscular with 6 small points around the rim. The thorax is contracted in the holotype. It has a strong retractor muscle from the posterior end of the thorax, and strong dorsal pharyngeal muscles. Bidentate atrial lips of various lengths project from the anterior rims of the atrial apertures. The gut loop forms a wide loop flexed ventrally. Gonads are not mature in the present specimen,

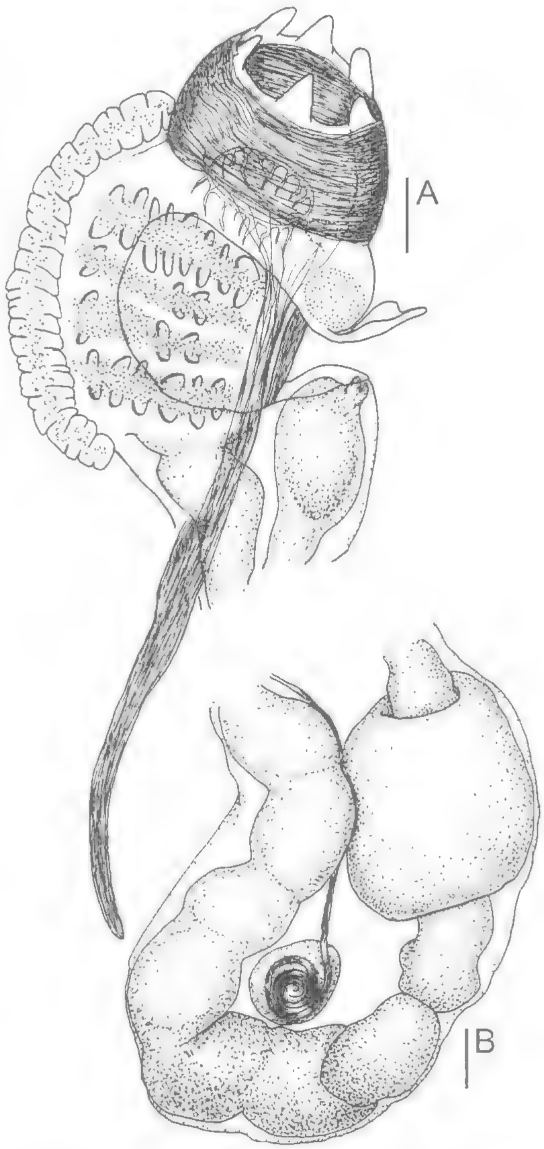


FIG. 66. *Polysyncraton scorteum* sp. nov. (SAM E2629) – A, thorax; B, abdomen. Scales: 0.1mm.

and the exact number of testis follicles was not determined. The vas deferens appears to have 3 coils.

REMARKS. Although the testis is not mature, the large zooids, each with strong thoracic muscles and a conspicuous atrial tongue, are typical of *Polysyncraton*. As well as the strong thoracic muscles and the form of the atrial tongue, the characteristics of the present species are its tough leathery colonies with large, globular, spicules crowded throughout.

The tropical *P. circulum* has similar spicules, both in size and form (although it is not known whether or not they are hollow in the present species). Again, they are not present throughout the colony as they are in the present species.

Polysyncraton sideris sp. nov.
(Figs 67, 165B)

Polysyncraton orbiculum Kott, 1962: 300 (part, specimens other than those from Mary Cove and Salmon Bay).

TYPE LOCALITY. Western Australia (Rottnest I., Fishhook Bay undercut, coll. P. Kott November 1951, holotype AM Y1483; Rottnest I., Cape Vlamingh, coll. P. Kott, paratype AM Y1480; Rottnest I., coll. P. Kott, paratype AM Y1487).

COLONY. Colonies are relatively firm, irregular plates, about 2cm in maximum dimension, with rounded margins and spicules crowded throughout. Spicules outline the margin of each stellate branchial aperture. Spicules in the surface test are interrupted by 12–15 conspicuous vesicles arranged in a wide circle around each aperture. Zooids retain their brown colour, even after long-term preservation, and can be seen through the branchial apertures. Distinct radial ribs of crowded spicules in the roof of the common cloacal cavity around each common cloacal aperture can be seen from the surface through the spicule-free thin test around each aperture. The common cloacal cavity is a deep, horizontal space with thoraces crossing it in their own spicule-filled sheath of test.

Spicules are large (to 0.14mm in diameter), stellate with 7–9 conical pointed rays in optical transverse section and a ray length/spicule diameter ratio of 0.4.

ZOOIDS. Zooids are delicate. Thoraces are distended in these specimens. Branchial siphons are relatively short with 6 narrow, pointed lobes. Atrial apertures are sessile with a small bifid tongue from the upper rim. A retractor muscle

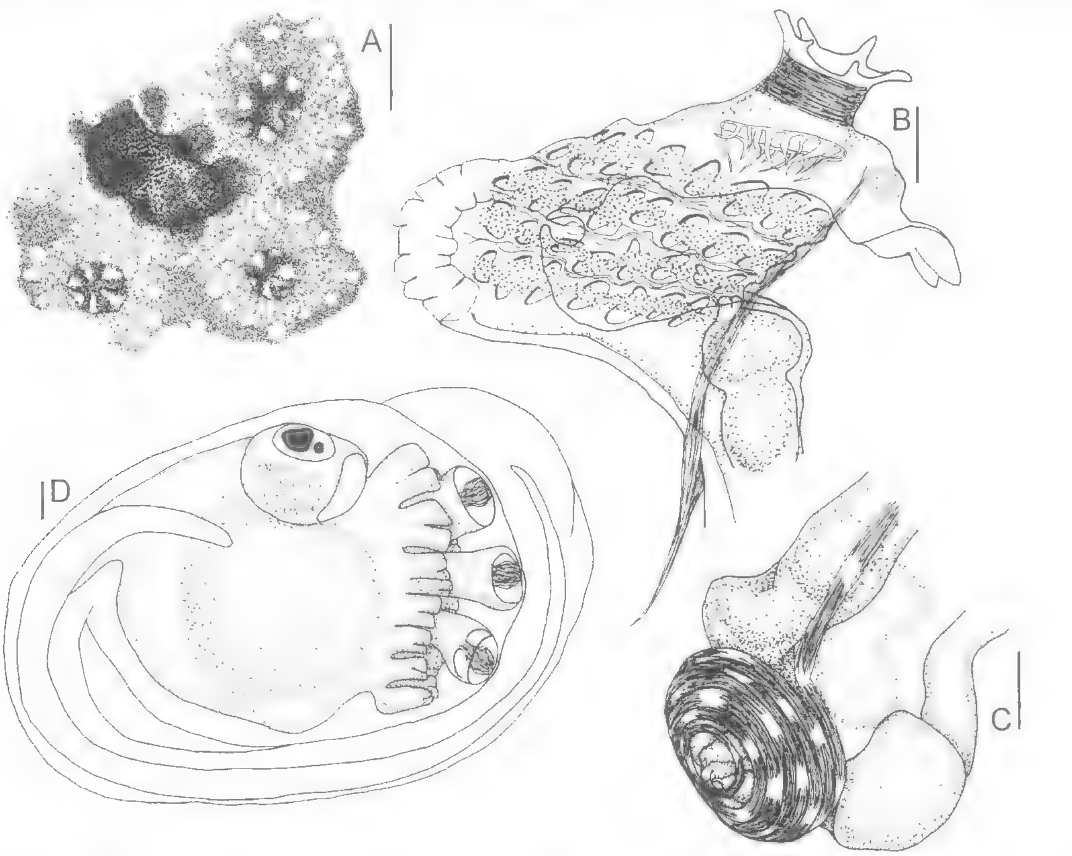


FIG. 67. *Polysyncraton sideris* sp. nov. (A, AM Y1480; B,C, AM Y1487; D, AM Y1483) – A, surface of colony showing common cloacal and branchial apertures, vesicles around each branchial aperture, and spicule distribution in branchial siphons and in radial ribs around common cloacal apertures; B, thorax; C, abdomen; D, larva. Scales: A, 0.3mm; B–D, 0.1mm.

projects from the oesophageal neck but was hard to detect. Large spherical lateral organs are everted from each side of thorax. About 8 stigmata are in each of the rows of the branchial sac. The gut forms a narrow loop, and 7 coils of the vas deferens surround the 5 testis follicles.

Large larvae with a yolky trunk 1.0mm long and relatively deep occur in the basal test of the holotype, collected in November. About 8 bilobed ectodermal ampullae are on each side of the 3 stout antero-median adhesive organs. Oozoids have 4 rows of stigmata and an otolith and ocellus in the cerebral vesicle. Blastozooids were not detected.

REMARKS. The species is sympatric with *P. orbiculum* and is readily confused with it, having similar circles of vesicles around each branchial aperture interrupting the spicules in the surface test. It is distinguished by its large (to 0.14mm diameter) spicules (which reach twice the size of the largest ones in *P. orbiculum*) and by the fewer and more pointed spicule rays. Other differences distinguishing *P. sideris* from *P. orbiculum* are more (12–15 rather than 8–10) vesicles around the branchial apertures, 7 (rather than 5) coils of the vas deferens and the clear margin of spicules outlining each branchial aperture. The colonies also are different, the present species having small, firm, plate-like colonies (rather than the more extensive sheets of *P. orbiculum*), and radial ribs around the cloacal apertures.

The greenish (in preservative) colonies of *P. tasmanense* (>*Didemnum mortenseni*: Kott, 1954) from the NE coast of Tasmania (AM Y1541) have similar spicules to the present species, but the largest is only 0.114mm in diameter and they have only 9–11 long, pointed rays. This species lacks vesicular cells and has irregular and complex colonies with outgrowths fusing with other parts of the surface. *P. mortenseni*: Kott, 1962 from Oyster Bay, Tasmania, has even larger spicules and is the holotype of *Leptoclinides magnistellus*.

Polysyncraton tasmanense sp. nov.
(Figs 68A, 164-I)

Didemnum mortensensi: Kott, 1954: 163 (part, from BANZARE Station 115).

TYPE LOCALITY. Tasmania (NE coast, BANZARE statn 115 676-128m, March 1931, syntypes AM Y1541).

COLONY. Colonies are thin and irregular, with solid but narrow cylindrical protrusions from some parts of the surface which occasionally overgrow it to form a complex 3-dimensional colony. Common cloacal canals are shallow and thoracic. Spicules are crowded throughout, large, stellate, to 0.114mm in diameter and with 9–11 conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.33. Tips of the rays are usually pointed but some are chisel-shaped and occasionally forked.

Colonies are pale green after long-term (nearly 70 years) perservation and the dark blackish-green zooids can be seen through the branchial apertures on the surface.

ZOOIDS. The size, contraction and dark colour of the zooids obscured their structure. Four rows of stigmata and a wide atrial opening without an atrial tongue were detected. Kott (1954) saw 5 male follicles and 2 coils of the vas deferens, although this was not confirmed on re-examination. Larvae are not known. Those shown in Kott (1954) are from the holotype of *Trididemnum cristatum*.

REMARKS. The species is erected on the basis of its unique coloured zooids, the size and form of its spicules, and its complex colony form. Although the spicules of *P. tegetum* are similar with a similar range in diameter and occasional chisel-shaped rays, they have more rays, and the zooids have more coils of the vas deferens. *P. sideris* has similar though smaller spicules but with fewer rays and is further distinguished by the vesicular cells in the surface test.

Polysyncraton tegetum sp. nov.
(Figs 68B,C, 164G)

Leptoclinides reticulatus: Kott, 1975: 8 (part).
Didemnum moseleyi: Kott, 1975: 9.

TYPE LOCALITY. South Australia (Great Australian Bight 32°24'S 133°30'E, coll. P. Symonds, Prawn Expedition 23.8.73, holotype SAM E2698; paratype, SAM E2664).

COLONY. In preservative colonies are thin, hard and investing sheets (SAM E2698) to cushions (about 1cm thick) with zooids crowded in the upper half (SAM E2664). Colonies are smooth and featureless without conspicuous branchial apertures, and are opaque and cream coloured with brownish transparent zooids. Spicules are less crowded in the superficial and the basal layers of test, than they are in the remainder of the colony. They are all stellate, but there is a great range in sizes (to 0.125mm, but usually less); and there are several different shapes. Many of the smaller spicules have 7–9 long, pointed (sometimes almost fusiform) rays in optical transverse section with a ray length/spicule diameter ratio 0.375-0.4, but the larger spicules have 11–13

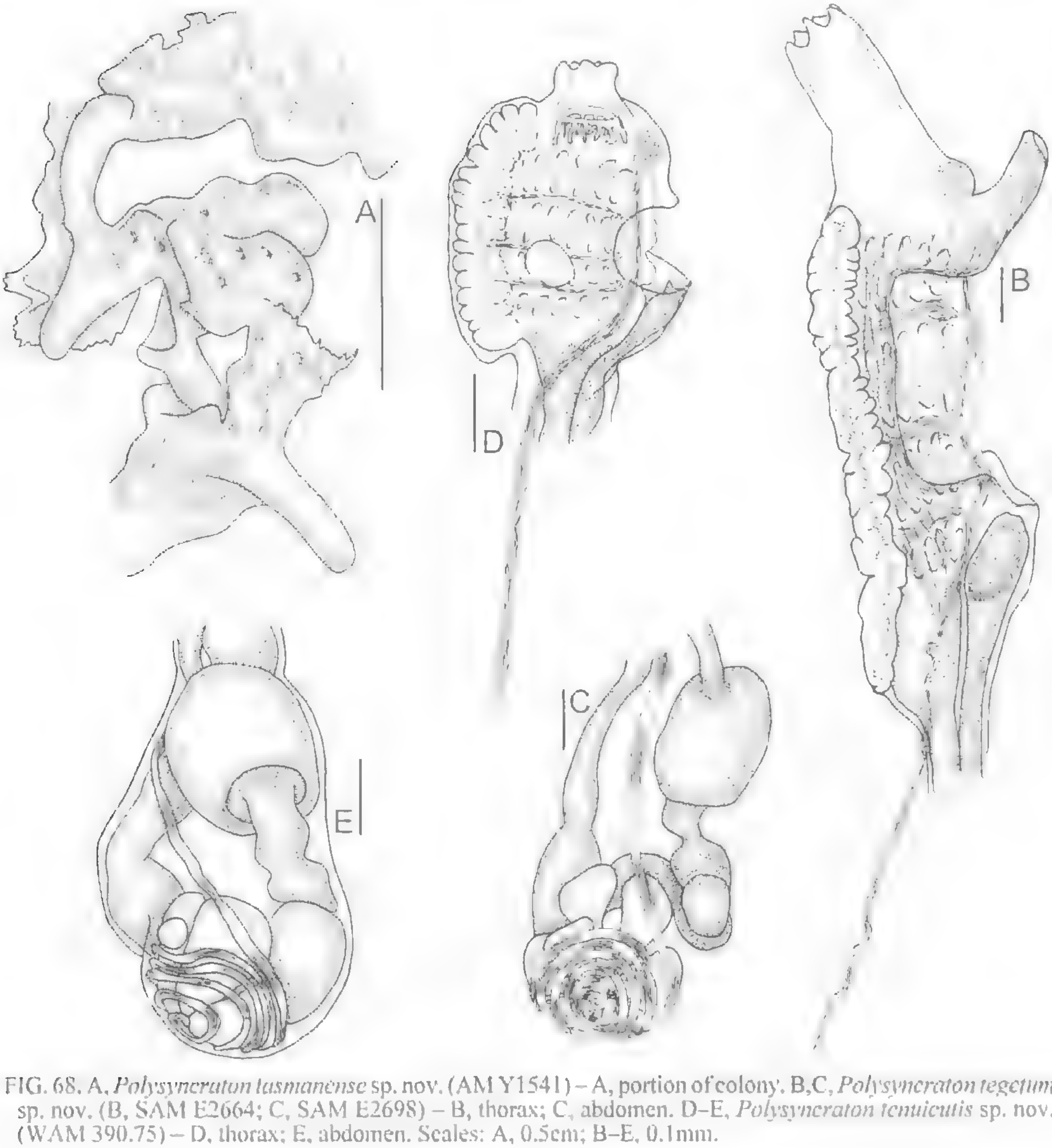


FIG. 68. A, *Polysyncraton tasmanense* sp. nov. (AM Y1541) – A, portion of colony. B,C, *Polysyncraton tegetum* sp. nov. (B, SAM E2664; C, SAM E2698) – B, thorax; C, abdomen. D–E, *Polysyncraton tenuicutis* sp. nov. (WAM 390.75) – D, thorax; E, abdomen. Scales: A, 0.5cm; B–E, 0.1mm.

well-spaced, but relatively short conical rays with a ray length/spicule diameter ratio of about 0.2. A few of the smaller spicules have shorter, even, conical tips widely separated from one another on the central spherical mass. Some of the spicule rays have chisel shaped tips.

Cloacal cavities were not detected, but probably are narrow canals at thorax level.

ZOOIDS. Zooids are about 1mm long. In the holotype abdomina are well-developed and 7 coils of the vas deferens surround up to 8 long club-shaped follicles. Vegetative buds are in the oesophageal region, but thoraces are disintegrating. The paratype which was taken at the same time, does not have mature testes, but the thoraces are large and well-preserved, with a relatively long branchial siphon, a distinct anterior atrial lip, a large lateral organ opposite the second row of stigmata (near the rim of the large sessile atrial aperture), and a long tapering retractor muscle from the anterior part of the oesophageal neck. Larvae are not known.

REMARKS. Characteristics of this species are its limited cloacal spaces, large lateral organs, relatively numerous vas deferens coils and testis follicles, and large crowded stellate spicules. Both holotype and paratype are from the Great Australian Bight. The holotype was assigned to *Leptoclinides reticulatus* (with a specimen of *Leptoclinides variegatus*) by Kott (1975). Kott (1975) had assigned the paratype to *Didemnum moseleyi*. Despite its lack of gonads, it has large thoraces, anterior lateral organs, atrial tongue and retractor muscle which together are characteristic of *Polysyncraton*, and its spicules are identical with those of the holotype.

P. infundibulum from South Australia has uniform, short-rayed stellate spicules with short conical rays, and they are smaller than those of the present species, never exceeding 0.075mm in diameter.

The three specimens of *Didemnum mortensi*: Kott, 1954 from the NE coast of Tasmania with large stellate spicules, belong to 2 different species. One (AM Y2321) is the holotype of *Trididemnum cristatum* and another (AM Y1542) may be the same species. The five male follicles and 3 to 4 coils of the vas deferens which Kott (1954) reported for *D. mortenseni* were not found in any of the re-examined material. They are unlikely to have been in the specimens assigned to *T. cristatum* but probably were in the small dark green zooids of the third specimen (AM Y1541) – the type specimen of *Polysyncraton tasmanense*. The latter species has fewer spicule rays than *P. tegetum* (see also *P. sideris*).

Polysyncraton tenuicutis sp. nov. (Figs 68D,E, 165D)

TYPE LOCALITY. Western Australia (W. of Long I., Wallabi Group. Houtman's Abrolhos, coll. L. Marsh et al., 27.10.74, holotype WAM 390.75).

COLONY. The preserved colony is a fragile, thin sheet, with spicules embedded throughout. A bladder cell layer was not detected on the surface of the colony, and the upper layer of test is thin and fragile, accommodating only a single layer of quite crowded spicules over the zooids. The common cloacal system consists of deep primary canals surrounding clumps of zooids and secondary cavities that penetrate into these clumps at thorax level. The primary cavities extend the whole length of the zooids, sometimes being post-abdominal, and a thin layer of basal test forms the floor of the cavity. The thin surface test is depressed over the deep primary canals. Conspicuously stellate branchial apertures lined with spicules, are evenly distributed over the surface of the colony.

Spicules are generally small, not more than 0.03mm diameter with about 9–11 short blunt-tipped rays in optical transverse section, although occasional larger ones (to 0.06mm diameter) have 12–14 long rod-like or almost club-shaped rays in optical transverse section and others, even larger (to 0.125mm diameter) are stellate with 5–7 thick, stumpy conical rays in optical transverse section. Also, fusiform or irregularly branched rods to 0.045mm long, occasionally occur amongst the spherical spicules.

ZOOIDS. Zooids in the holotype are about 1.0mm long with contracted thoraces in which it was not possible to determine the number of stigmata. The branchial siphon is short, with rounded lobes and the atrial opening is large and sessile, exposing much of the branchial sac directly to the atrial cavity. An atrial tongue is not present. A long, tapering, strong retractor muscle projects free of the zooid from the upper half of the oesophageal neck. The post-pyloric part of the gut loop is flexed ventrally. A large egg is present at the posterior end of the zooid against the flexed part of the gut loop and a few zooids have a mature testis consisting of 4 large follicles surrounded by 5 coils of a thick vas deferens. Embryos are not present in the test. It is probable that the species is protandrous.

REMARKS. The principal distinguishing character is the large stellate spicules with very few rays scattered amongst the others. Other species of *Polysyncraton* with a similar diversity of spicules crowded throughout the test are *P. oceanium* and *P. magnetae*. Generally the majority of spicules in the present species are smaller than in *P. oceanium*, they are about the same size as in *P. magnetae* but lack the acutely pointed rays that occur in the latter species. Further, in *P. oceanium* a superficial layer of bladder cells obscures the surface depressions over the deep primary cloacal cavities and creates a thicker and firmer surface layer.

P. jugosum has small, crowded, stellate spicules and some globular ones together with a few large (to 0.08 diameter) stellate ones. The latter have more rays than the stellate spicules of the present species, and the smaller ones have more pointed rays.

Genus **Didemnum** Savigny, 1816

TYPE SPECIES. *Didemnum candidum* Savigny, 1816.

The genus is characterised by relatively small zooids (often not more than 1mm long); 4 rows of stigmata (seldom with more than 8 per row); a large sessile atrial aperture exposing much of the dorsal surface of the pharynx directly to the cloacal cavity; vas deferens coiled tightly around the testis which usually is undivided or (occasionally) divided into 2 equal halves as in *D. bimasculum* Monniot, 1995, *D. bisectatum*, *D. rubeum* Monniot & Monniot, 1996 and *D. uturoa* Monniot & Monniot, 1987 and a number of species from the northern Pacific Ocean (Romanov, 1989; Sanamyan, 1999. A retractor muscle usually projects from the oesophageal neck of each zooid; and calcareous spicules are present in some or all parts of the test of most species, being entirely absent only in exceptional cases (see *D. effusium*, *D. jedanense*).

Sometimes a small, often bifid, atrial lip (or tongue) projects from the anterior rim of the atrial aperture. The gut is divided into oesophagus, almost spherical stomach, a duodenal region (often expanded distally), a short posterior stomach and a long rectum. The rectum usually is divided into a roomy proximal chamber and a narrow distal tube separated by a short constriction surrounded by inconspicuous tubules of the gastro-intestinal gland. The relatively short gut loop often has the distal post-pyloric part bent ventrally to form an angle with the proximal part, or even bent up against the proximal part to form a secondary loop. Gonads are dorsal to or (when it is ventrally flexed) posterior to the distal part of the gut loop. The ascending limb of the gut loop often is kinked up anteriorly over the testis.

The thoracic body wall musculature consists of fine parietal longitudinal bands extending along each side of the atrial aperture, transverse muscle fibres between the rows of stigmata, a strong dorsal pharyngeal muscle on each side of the dorsal mid-line, a retractor muscle, and a branchial sphincter. *D. fucatum* is an exception in having an oesophageal constrictor and no retractor muscle. Transverse muscles are not in the parietal body wall. A sphincter muscle surrounds the atrial opening only in *D. fucatum*, the only *Didemnum* species known to have a posteriorly placed, circular atrial aperture, although it is sessile and does not project on a siphon as in *Leptoclinides* and most *Trididemnum*.

In the majority of species, the lateral organ is in the parietal body wall level with the third row of stigmata. Its displacement to positions opposite the second to the fourth rows of stigmata can result from contraction of the body wall muscles, including the upper part of the retractor muscle. When the atrial aperture is open wide the lateral organs appear to project from each side of the opening (from each side of the endostyle). Two or 3 often inconspicuous stolonic test vessels of variable length, each with a terminal bulb-like expansion (ampulla) project from the ventral concavity of the abdomen, opposite the centre of the gut loop (Millar, 1951).

Larvae are relatively small, seldom more than 1mm, with 4 or 5 pairs of lateral ampullae each side of the 3 antero-median adhesive organs. In a few species, lateral ampullae are more numerous, 8–10 on each side (*D. arancium*, *D. caesium*, *D. chartaceum*, *D. clavum*, *D. jedanense*, *D. multispirale*, *D. precocinum* and the Atlantic species *D. cineraceum* Monniot, 1993). With the exception of *D. clavum*, *D. caesium* and *D. multispirale* in which adult organs are not well advanced in the known larvae, the species listed are amongst the few *Didemnum* spp. with precocious blastozooids in the larval trunk. *D. ossium*, the Atlantic species *D. ligulum* Monniot, 1983, and Indonesian *D. guttatum* Monniot & Monniot, 1996 and *D. linguiferum* Monniot & Monniot, 1996 have a corolla of 30 ectodermal ampullae circling the anterior end of the trunk. The larval pharynx has 3 rows of stigmata in the oozooid, but 4 in the blastozooids. Occasionally only 2 adhesive organs are present as in *D. albopunctatum*, *D. parancium*, *D. pitipiri* Monniot & Monniot, 1987, *D. poecilomorpha*, *D. dicolla* Monniot, F. & Monniot, C., 1997 from Tanzania, *D. maculosum* (Milne Edwards, 1841) from the northern Atlantic and *D. risirense* Nishikawa, 1990 from Japan. Generally the larval trunk is thick and rounded at each end, rather than attenuated posteriorly (where the tail is inserted) as in *Trididemnum*.

Colonies with more than one cloacal system usually are thin, encrusting sheets or extensive irregular masses, their upper surface elevated into rounded or irregular lobes with terminal common cloacal apertures. Regular cushion or vase-shaped colonies each consisting of a single cloacal system with a terminal or central excurrent aperture are known. Some with the latter type of colony are known to clone (subdivide: see *D. molle*). The surface of *Didemnum* colonies often is smooth, but

occasionally minute spicule-filled papillae are crowded on the whole or some parts of the surface between the branchial apertures. In several species (*D. clavum*, *D. cuculliferum*, *D. cygnus*, *D. membranaceum*, *D. scopi* and *D. stragulum*) a small pointed papilla, into which an enlarged ventral lobe of the branchial aperture is inserted, is associated with some or all of the zooids on some or all of the colonies and is pulled down over the openings when the zooid contracts (see also *Polysyncraton echinatum*).

Cloacal systems usually are extensive with relatively shallow 2-dimensional horizontal cavities penetrating the test at thoracic level. Although 3-dimensional cavities (thoracic cavities), extending into large posterior-abdominal spaces behind the zooids, also occur they are not common and are present only in the more bulky, upright colonies, including vase-shaped or lobed ones where cloacal spaces are crossed by test connectives from the surface zooid-bearing layer of the colony to a basal layer or a central test core. Spicules usually are present throughout but sometimes are absent from parts of the colony. Very occasionally the colony is aspicular (e.g. *D. effusium*, some colonies of *D. jedanense*). In *D. clavum* , *D. cuculliferum* and *D. membranaceum* occasional spicules are tetrahedral or have 4–6 narrow pointed rays. Generally spicules have more numerous conical, rounded or rod-like (cylindrical) rays and are stellate, globular, or burr-shaped. Maximum diameter of spicules ranges from 0.02 to about 0.1mm. Bladder cells are present in the test, often in a superficial layer, but sometimes throughout (e.g. *D. chartaceum*).

Living colonies usually are brightly coloured, ranging from red, through orange, yellow, blue, and violet shades, as well as green, black and brown. The pigment occurs in irregular, fusiform to spherical cells in the surface test, mixed with spicules. Pigment usually is lost in preservative. In some species dark spherical cells in larval and adult haemocoel and around the zooids, affect the internal colour of the preserved colonies (see Glossary, **haemocoel**).

Several tropical species have obligate symbioses with chlorophyll-containing cells. One of the most commonly encountered, *D. molle*, with an extensive geographic range from the western Indian Ocean to Fiji between about 26°N and 32°S, has a well established relationship with the prokaryotic alga *Prochloron* Lewin, 1977, the algal cells being present in the common cloacal cavity. Small, less conspicuous *D. etiolum* and *D. flavoviride*, with *Prochloron* symbionts embedded in the test, are less often recorded — possibly overlooked. Large sheet-like colonies of *D. verdantum* also may have *Prochloron* symbionts, although other sheet-like species, *D. viride*, *D. guttatum*, *D. herba* and possibly *D. poecilomorpha* have a similar symbiosis with cyanophytes in the test. Other tropical species sometimes have patches of non-obligate symbionts, usually *Prochloron*, on the surface (Kott et al., 1984).

Characters described above are not unique — all occur in one or more genera of the Didemnidae. It is the combination of characters that determine *Didemnum*. *Lissoclinum* and *Diplosoma*, with a straight rather than coiled vas deferens are readily distinguished from *Didemnum*. Although there are exceptions, *Leptoclinides* has larger zooids, more fleshy colonies and more extensive posterior abdominal cloacal cavities than *Didemnum*, and always it has an atrial siphon, and lacks a retractor muscle. *Trididemnum* zooids also have an undivided testis, a coiled vas deferens and a retractor muscle, but usually (though not always) are smaller than zooids of *Didemnum*, have only 3 rows of stigmata and usually a posteriorly oriented atrial siphon.

Monniot (1995) believes that separation of *Polysyncraton* (with numerous male follicles) from *Didemnum* (with the testis undivided or divided into 2) is arbitrary, justified only on practical rather than phylogenetic grounds. This is not a view supported by material examined in the present study. A relatively few *Didemnum* spp. have some *Polysyncraton* characters (such as an atrial lip and relatively large zooids, as well as large larvae with 8 or more pairs of ectodermal ampullae and blastozooids). This may be an indication of convergence or even affinity, but not evidence of congeneric taxa. Generally, in *Polysyncraton*, zooids are larger than those of *Didemnum*, with fewer and looser coils of the vas deferens, a number of rather loosely associated club-shaped male follicles, adult organs less well developed in the larvae than in *Didemnum* and other genera and 4 (rather than 3) rows of stigmata in the larval oozooid.

Species of *Didemnum* can be distinguished from each other by the form of the colony and its colonial systems, distribution size and form of spicules, distribution of bladder cells in the test, length of the branchial siphon and shape of

branchial lobes, presence or absence of an atrial languet, form of the lateral organ, size of the zooids and number of stigmata, number of coils of the vas deferens, length of the gut and flexure of the posterior pyloric part of the loop. The most reliable characters are the size, form and distribution of spicules. Also significant are the number of larval ectodermal ampullae, and the presence or absence of precocious blastozooids in the larval trunk. However, one of the most variable characters is the size of the larval trunk, intraspecific variations in its length often being recorded, and species determined only on that basis are not reliable. Further, most larvae described from French Polynesia (Monniot & Monniot, 1987) have a larval trunk less than 0.4mm long. It is unlikely that the French Polynesian ascidian population consists only of species with larval trunks less than 0.4mm. It is more likely a characteristic associated with partial isolation of these populations.

Didemnum is diverse and cosmopolitan, occurring around all continents, including polar waters, although deep slope or abyssal species are not known. The geographic range of many species is extensive, an Indo-West Pacific range not being unusual for tropical species. Circumpolar species, although less diverse, are well documented for the Southern Ocean (see Kott, 1969). Many of the tropical Australian species have also been recorded from the western Pacific islands including Indonesia. Of the 20 species recorded from French Polynesia only 2 have not been recorded from other western Pacific locations. Only 5 of the 30 species recorded from New Caledonia (Monniot, 1995) are known only from that location. They will very likely be found to occur elsewhere as further collecting is done and new habitats explored. However, it is not likely that larvae are free-swimming for long periods, since sometimes they are found metamorphosing in the parent colony. Gene flow may occur through transport by driftwood and possibly by delayed metamorphosis. Indigenous temperate species abound in Australian waters however (see Glossary, **gene flow**).

Many of the *Siboga* specimen lots (Sluiter, 1909; Spoel, 1969) have been re-examined and in some cases have been found to consist of more than one species (see Table 3) emphasising the problems of identification.

KEY TO SPECIES OF *DIDEMNUM* RECORDED FROM AUSTRALIA

(T indicates a temperate species)

1. Atrial aperture small, posterior, and does not expose a large part of the branchial sac directly to the cloacal cavity . . . . *D. fucatum*

   Atrial aperture large, and exposes a large part of the branchial sac to the cloacal cavity 2

2. Green cell symbionts crowded in common cloacal cavity or embedded in test. 65

   Green cell symbionts not crowded in common cloacal cavity or embedded in test. 3

3. Faecal pellets embedded throughout . . *D. psammatode*

   Faecal pellets not embedded throughout 4

4. Spicules include elongate bilaterally symmetrical ones with some conspicuously enlarged rays; never aspicular . . . . *D. uturoa*

   Spicules never elongate, bilaterally symmetrical with conspicuously enlarged rays; occasionally aspicular . . 5

5. Spicules globular or burr-like or if stellate the maximum number of rays 15 or more in optical transverse section; or colonies aspicular 6

   Spicules mainly stellate, never with more than 13 rays in optical transverse section; colonies never aspicular . 28

6. Spicules mostly globular or burr-like with rod-like, fusiform, or irregular rays, or aspicular 7

   Spicules mostly stellate with regular conical rays, never aspicular. 17

7. Spicule rays thick, 9–11 in optical transverse section; never aspicular . . . . *D. oblitum* sp. nov.

   Spicule rays thin, more than 11 in optical transverse section; or aspicular. 8

8. Spicules include some with short points isolated on central sphere; never aspicular . . *D. arancium* sp. nov.

   Spicules do not include any with short points isolated on central sphere; or aspicular 9

9. Bladder cells in conspicuous spicule-free superficial layer over spicules; 9 coils of vas deferens; never aspicular. 10

   Bladder cells not in a conspicuous spicule-free layer over spicules; less than 9 coils of vas deferens; or aspicular. 11

10. Cloacal systems numerous, sheet-like colony with crowded spicules . . . . *D. albopunctatum*

    Cloacal systems one or 2 in small plate-like colony with sparse spicules . . . . *D. hiopaa*

11. Spicules to 0.06mm or more diameter; never aspicular 12

    Spicules not more than 0.04mm diameter; or aspicular 13

12. Atrial tongue present; 6 coils of the vas deferens. . . . . *D. precocinum* sp. nov.

    Atrial tongue not present; 8 coils of the vas deferens. . . . . *D. theca* sp. nov.

13. Zooids only along each side of circular common cloacal canals. . . . . *D. jedanense*

    Zooids not only along each side of circular common cloacal canals 14

14. Colonies aspicular . . . . *D. effusium* sp. nov.T

    Colonies not aspicular 15

15. Spicules to more than 0.02mm diameter; colony sheet-like 16

Spicules not more than 0.02mm diameter; colony spherical . . . . *D. monile* sp. nov.[T]

16. Larvae with 4 pairs of ectodermal ampullae . . *D. fragile*

Larvae with 3 pairs of ectodermal ampullae . . . . *D. parancium* sp. nov.

17. Spicules not present throughout colony. 18

Spicules present throughout colony. 19

18. Spicules with more than 19 rays in optical transverse section . . . . *D. chartaceum*

Spicules with not more than 19 rays in optical transverse section . . . . *D. levitas* sp. nov.

19. Common cloacal cavity partly posterior abdominal . . . . *D. ternerratum* sp. nov.[T]

Common cloacal cavity never posterior abdominal . . 20

20. Spicules to more than 0.04mm diameter 21

Spicules never more than 0.04mm diameter. . . . . *D. bicolor* sp. nov.[T]

21. Vas deferens coils 12 times. . . . *D. jucundum* sp. nov.[T]

Vas deferens coils less than 12 times 22

22. Spicules include globular ones with flat-tipped rays . 23

Spicules do not include globular ones with flat-tipped rays 25

23. Testis subdivided . . . . *D. bisectatum* sp. nov.

Testis not subdivided 24

24. Conical spicule rays separated from one another on central mass . . . . *D. multispirale* sp. nov.

Conical spicule rays not separated from one another on central mass . . . . *D. astrum* sp. nov.

25. Spicule rays 17 – 19 in optical transverse section . . . 26

Spicule rays 13 – 15 in optical transverse section . . . . *D. vahatuio*

26. Spicule ray-length/diameter ratio 0.4 . . . *D. tabulatum*

Spicule ray-length/diameter ratio less than 0.4 27

27. Spicule rays all conical; spicule rays never crowded basally . . . . *D. mutabile*

Spicule rays not all conical; spicule rays often crowded basally. . . . . *D. lacertosum*

28. Free dark brown spherical cells present around zooids 29

Free dark brown spherical cells not present around zooids 31

29. Spherical vesicles interrupt spicules around branchial apertures . . . . *D. spadix* sp. nov.[T]

Spherical vesicles do not interrupt spicules around branchial apertures. 30

30. Spicules to more than 0.07mm diameter . . . *D. fuscum*

Spicules not more than 0.07mm diameter . . . . *D. sordidum* sp. nov.

31. Occasional giant spicules with a total of 4–6 rays present 32

Occasional giant spicule with a total of 4–6 rays not present. 35

32. Giant spicules with broad-based conical rays . . . . *D. complexum* sp. nov.[T]

Giant spicules with long spiky rays 33

33. Stigmata 6 in anterior row. 34

Stigmata 9 in anterior row . . . . . . *D. clavum* sp. nov.

34. Spicules to 0.06mm diameter with conical pointed rays; vas deferens with 6 coils; ray length/spicule diameter ratio 0.3 or less . . . . *D. membranaceum*

Spicules not more than 0.04mm diameter with rod-like blunt-tipped rays; vas deferens with 8 coils; ray length/spicule diameter ratio 0.4 . . . . *D. cuculliferum*

35. Spicules sparse in or absent from appreciable parts of the colony 36

Spicules not sparse in or absent from appreciable parts of the colony 43

36. Colonies upright lobes with terminal common cloacal apertures; posterior abdominal cavities always present 37

Colonies not upright lobes with terminal common cloacal apertures; posterior abdominal cavities not always present 41

37. Spicules all less than 0.07mm diameter 38

Spicules not all less than 0.07mm diameter 39

38. Spicule rays to 13 in optical transverse section; larval trunk 0.9mm long with 6 ectodermal ampullae per side . . . . *D. fragum* sp. nov.[T]

Spicule rays to 11 in optical transverse sections; larval trunk 0.5mm long with 5 ectodermal ampullae per side . . . . *D. pecten* sp. nov.[T]

39. Branchial siphon about half the length of the thorax or more; 12 or more larval ectodermal ampullae per side . . . . *D. pellucidum* sp. nov.[T]

Branchial siphon less than half the length of the thorax; fewer than 12 larval ectodermal ampullae per side . . 40

40. Spicules to more than 0.1mm diameter and 9–11 rays in optical transverse section. . . . . *D. sucosum* sp. nov.[T]

Spicules not more than 0.1mm diameter and 7–9 rays in optical transverse section. . . . . *D. roberti*

41. Dark pigment persists in surface of preserved specimens; common cloacal cavity thoracic only . . . . *D. caesium*

Dark pigment not present in surface of preserved specimens; common cavity not only thoracic 42

42. Zooids in ligament between surface and basal test. . . . . *D. linatum* sp. nov.

Zooids in double series along each side of circular cloacal canals. . . . . *D. cygnuus* sp. nov.

43. Colony a single cloacal system . *D. minisculum* sp. nov.[T]

Colony not a single cloacal system 44

44. Cloacal cavities include posterior abdominal component 45

Cloacal cavities do not include posterior abdominal component. 49

45. Branchial siphons about half the length of the thorax . . . . *D. elongatum*

Branchial siphons significantly less than half the length of the thorax 46

46. Colonies sheet-like; lateral organ flap-like . . . . *D. crescente* sp. nov.[T]

Colonies usually lobed, branched forming complex reticulum; lateral organ not flap-like 47

47. Spicules with rounded as well as conical rays . . . . *D. ossium* sp. nov.

Spicules with conical rays only 48

48. Outer surface with vertical toothed ridges . . . . *D. spongioide*

Outer surface smooth . . . . . . *D. lissoclinum* sp. nov.[T]

49. Bladder cell layer containing dark pigment conspicuous on surface . . . . *D. grande*

Bladder cell layer containing dark pigment not conspicuous on surface 50

50. Spicules to 0.09mm diameter or more 51
Spicules not more than 0.07mm diameter . . . 53
51. Branchial apertures each associated with a pointed surface papilla . . . . *D. stragulum* sp. nov.
Branchial apertures not associated with a pointed surface papilla 52
52. Atrial lip present; some spicules with blunt or truncated rays present . . . *D. inveteratum* sp. nov.
Atrial lip not present; spicule rays never blunt or truncated . . . . *D. microthoracicum* sp. nov.[1]
53. Surface marked off into polygonal areas by depressions over primary cloacal canals . . . 54
Surface not marked off into polygonal areas by depressions over primary cloacal canals 58
54. Branchial siphons longer than half the length of the thorax . . . *D. macrosiphonium* sp. nov.[1]
Branchial siphons not longer than half the length of the thorax 55
55. Spicules of 2 types, some with rod-like rays, others conical. *D. tonga*
Spicules not of 2 types, conical rays only present . . . 56
56. Ray length/spicule diameter ratio more than 0.3 . . . 57
Ray length/spicule diameter ratio less than 0.3 . . . . *D. pardum*[1]
57. Vas deferens coils 11 times around testis . *D. via* sp. nov.
Vas deferens coils 9 times or less around testis. . . . . *D. mantile* sp. nov.[1]
58. Spicules mostly or only with rod-like rays 59
Spicules not mostly or only with rod-like rays. . . . 60
59. Spicules with 9 or more rays in optical transverse section . . . . *D. scopi* sp. nov.
Spicules never with more than 9 rays in optical transverse section . . . . *D. candidum*
60. Spicules with rounded and pointed conical rays and appreciable numbers of globular ones . . . *D. moseleyi*
Spicules rays mostly pointed conical-rays only 61
61. Spicules to 0.04mm diameter or less 62
Spicules to more than 0.04mm diameter 63
62. Vas deferens with 9 coils . . . *D.* [illegible]
Vas deferens with 6 coils . . . . *D. delectum*[1]
63. Spicule rays to 11 in optical transverse section . . . . . . *D. vulgare* sp. nov.[1]
Spicule rays to 9 or less in optical transverse section 64
64. Vas deferens coils 7 times. . . . . *D. perplexum* sp. nov.
Vas deferens coils 6 times . . . . *D. granulatum*
65. Spicules globular or burr-like only 66
Spicules not only globular or burr-like 67
66. Colony upright, vase-shaped; conspicuous quantity of mucus secreted when disturbed . . . . *D. molle*
Colony not upright, vase-shaped; mucus not secreted when disturbed . . . . *D. flavoviride*
67. Colonies small, inconspicuous with a single system . . . . *D. etiolum*
Colonies large, sheet-like with numerous systems . . . 68
68. Branchial siphon half the length of the thorax or more . . . 69
Branchial siphon less than half the length of the thorax . 71
69. Spicules with blunt-tipped as well as conical rays. . . . 70
Spicules only with pointed conical rays . . . . . *D. herba* sp. nov.
70. Spicule rays 9–11 in optical transverse section . . . *D.* [illegible]
Spicule rays 11–13 in optical transverse section . . . *D. poecilomorpha*
71. Spicule rays conical . . . *D. viride*
Spicule rays rod-like . . . *D. verdantum* sp. nov.

The following species known in adjacent areas are not yet recorded from Australian waters:

Didemnum apuroto Monniot & Monniot, 1987 (but not 1996); and Monniot (1995), has groups of zooids in unusual fused capsules of test and spicules. Spicules are up to about 0.03mm diameter, some with flat tipped truncated rays and others with pointed conical rays, 7–9 in optical transverse section. The vas deferens coils 6 times. The spicules resemble those of *D. diffundum* Monniot, 1995 (> *D. apuroto*: Monniot & Monniot, 1996), and the temperate *D. bicolor*. The former has more coils of the vas deferens (9) and the colonies are lobed with terminal common cloacal apertures. The latter has different cloacal systems from the present species. The blister-like capsules protruding from the surface occur in some specimens of *D. fragile* and they may have pathological rather than genetic significance.

Didemnum bimasculum Monniot, 1995 from New Caledonia have large (to 0.1mm diameter) spicules with 5–7 relatively short conical pointed rays in optical transverse section. The ray length/spicule diameter ratio is about 0.28. Although spicules resemble those of *D. caesium* and *D. grande*, the present species has a characteristic 2- lobed testis, larvae with 4 bifid ampullae on each side and green plant cells, probably in obligate symbiosis, embedded in the test and in the cloacal cavity. The other species with 2 male follicles recorded from this region are *D. recurvatum* Sluiter, 1909 (and possible synonyms *D. rubeum* Monniot & Monniot, 1996 and *D. fragile* Sluiter, 1909 part, ZMA TU446.2) which has small globular spicules with numerous rod-like rays; *D. biscetatum* and specimens from Kiribati assigned to *D. candidum*: Tokioka, 1967 with many rays on the stellate spicules; and *D. uturoa* (with unusual enlarged spicule rays).

Didemnum breviorıs Monniot, F. & Monniot, C., 1997 from the western Indian Ocean, has brown zooids with dark squamous epithelium possibly like those of *D. albopunctatum*. The small globular spicules most closely resemble those of *D. oblitum*. However, the species is distinguished by its small larval trunk (0.4mm long) with oozooid and blastozooid.

Didemnum captivum Monniot, F. & Monniot, C., 1997 from Tanzania, has a relatively large branchial sac with 8 stigmata in the anterior row, and possibly 8 coils of the vas deferens. The spicules with 7–9 conical rays to 0.04mm diameter resemble those of *D. candidum* from which it is distinguished by its 8 or 9 larval ectodermal ampullae per side and larval trunk 0.6mm long. *D. perplexum* is distinguished only by having fewer larval lateral ampullae and only 7 coils of the vas deferens. *D. granulatum* also has similar spicules but only 6 vas deferens coils and smaller larvae with 4 ectodermal ampullae per side.

Didemnum contortum Monniot, F. & Monniot, C., 1997 from Tanzania has spicules about the same size (to 0.03mm diameter) and form (with 17–19 pointed rays) as those of *D. tabulatum*. The species are distinguished by the more open cloacal systems in the Tanzanian species. In *D. contortum*, the common cloacal apertures are on the elevations formed by thickening of the sponge-like basal test which is filled with spicules and interrupted by cavities. Clumps of zooids are contained in test strands that interrupt a large common cloacal cavity and connect surface to basal test. The common cloacal cavity penetrates amongst the zooids at thoracic level. The zooids have a coiled vas deferens and a forked atrial lip. The cloacal systems resemble those of *Lissoclinum* spp., and some other species of *Didemnum* (e.g. the temperate *D. lissoclinum* and *D. ossium*, and *D. roberti* and *D. spongioide* from northern Australia), which have larger spicules with fewer rays than *D. contortum*.

Didemnum dealbatum Sluiter, 1909 from Indonesia was reported to be a fleshy irregular mass on sand and coral with a smooth upper surface and spherical spicules in the upper and lower layers of test (Sluiter, 1909). On re-examination, one of the syntype lots (ZMA TU441.1) was found to contain 2 colonies of a species of *Didemnum* and the other specimens (ZMA TU441.2), previously thought to be syntypes of the present species, were found to be 2 colonies of *T. miniatum* Kott, 1977 — small, soft, irregular colonies with rounded margins, minute zooids with 3-rows of about 7 stigmata, small larvae with the trunk surrounded by a coat of embedded symbionts, and globular spicules to 0.035mm diameter (but generally smaller). Thus only ZMA TU441.1 colonies constitute the syntypes of *D. dealbatum* (Spoel, 1969: pl. 1 fig 6). They are extensive flat sheets with an even upper surface stiff with crowded spicules. The upper surface is slightly wrinkled in preservative probably owing to the natural elasticity of the colony after its removal from the substrate. Another thin layer of spicules is on the base of the colony, but spicules are absent between. The spicules are stellate, up to 0.04mm diameter with about 11–13 longitudinally striated, sometimes pointed, rays in transverse optical section. Spicules are similar to but significantly smaller than those of *D. astrum*, which has similar cloacal cavities with zooids in clumps surrounded by deep cloacal cavities and some shallow secondary cloacal spaces at thoracic level, although in the latter species spicules are in a thicker layer in the upper part of the colony. The colonies look rather like *Leptoclinides brandi* owing to the stiff slightly wrinkled surface test over the gelatinous spicule-free test in the centre of the colony.

Didemnum dicolla Monniot, F. & Monniot, C., 1997 from Tanzania has thin encrusting colonies with shallow thoracic common cloacal cavities. Spicules are to 0.05mm diameter and have 9–11 pointed or truncated rays in optical transverse section. Zooids have a distinct double gut loop and 5 coils of the vas deferens. The larva has only 2 adhesive organs and 6 or 7 lateral ampullae on each side. Both common cloacal systems and spicules resemble those of *D. apuroto* Monniot & Moniot, 1987 and *D. diffundum* Monniot, 1995, but both these species have only 4 larval ectodermal ampullae (rather than 7 or 8 per side), 3 adhesive organs and more coils of the vas deferens. *D. albopunctatum*, *D. parancium*, *D. pitipiri* and sometimes *D. poecilomorpha* with only 2 larval adhesive organs have different spicules.

Didemnum diffundum Monniot, 1995 (> *D. apuroto*: Monniot & Monniot, 1996) from New Caledonia has spicules to 0.03 diameter with pointed as well as truncated rays that resemble those of *D. bicolor* but with fewer rays. Unlike *D. apuroto* (which also has similar spicules), *D. diffundum* has 9 coils of the vas deferens. *D. inveteratum* and *D. ossium* have similar but larger spicules than the present species.

Didemnum digestum Sluiter, 1909 from Indonesia, Fiji (Kott, 1981) and French Polynesia (Monniot & Monniot, 1987) resembles *D. uturoa* in the 1 to 3 enlarged rays on many of the spicules. Kott (1981) re-examined the spicules of the paralectotype of Sluiter's species (ZMA TU442.2) and found many of the spicules to have stumpy conical rays in polygonal bases in addition to the 1 or 2 large tapering rays; others are stellate with only 5–7 conical pointed rays in optical transverse section. Burr-like shapes with relatively numerous rays dominate the spicules of *D. uturoa*. The spicules of *D. digestum* are larger than *D. uturoa*, being up to 0.055mm in diameter.

Didemnum lambitum Michaelsen, 1924 from New Zealand resembles *D. fragum* from southern Australia in the large conical colonies with terminal common cloacal apertures and is distinguished from it principally by its shorter branchial siphon, 10 (rather than 12) coils of the vas deferens and 4 (rather than 6) larval ectodermal ampullae.

Didemnum ligulum: Monniot & Monniot, 1987 (part: flat, rose-coloured colonies) from French Polynesia is possibly an undescribed species with zooids grouped around a central aperture forming separate cloacal systems isolated from one another by narrow circles of zooid-free test. They resemble the isolated systems of *Polysyncraton glaucum* from which the French Polynesian specimens are distinguished by generic characters (gonads) and spicules (to 0.06mm diameter) with more (13 to 15 in optical transverse section), long and pointed, as well as truncated, rays. Spicules also distinguish the present species from the Atlantic nominal species (Monniot, 1983) and other specimens from French Polynesia (*D. arancium*) which Monniot & Monniot (1987) had thought were conspecific. The latter has small globular or burr-like spicules with numerous short points. The spicules resemble and are the same size as the spicules of *D. ossium* (>*D. ligulum*: Monniot, 1995) and *D. astrum*, but the cloacal systems are all different. Larvae are not known.

Didemnum linguiferum Monniot & Monniot, 1996 has thin, encrusting colonies with a red and white marbled surface, extensive thoracic common cloacal spaces, spicules crowded throughout, short branchial siphons, narrow thoraces, 6 stigmata in the anterior rows, 6 coils of the vas deferens, long (0.8mm) larval trunk with a circle of about 30 ampullae around the median adhesive organs and large (to 0.08mm diameter) stellate spicules with 15–17 conical points in optical transverse section. The spicules

TABLE 3. Siboga Expedition *Didemnum* spp. assigned by Sluiter (1909) and re-examined in the course of the present study.

Species assignation (Sluiter, 1909)	Specimen lot ZMA reg. no. (Spoel, 1969)	Revised assignation (this work)
D. albopunctatum	TU433.1	*Didemnum perplexum* sp. nov.
	TU433.2	lectotype *Didemnnum albopunctatum*
	TU433.3	*Didemnum multispirale* sp. nov. + *D. jedanense*
	TU433.4	*Didemnum jedanense*
D. caesium	TU434	holotype *Didemnum caesium*
D. chartaceum	TU437	syntypes *Didemnum chartaceum*
D. cuculliferum	TU490	holotype *Didemnum cuculliferum*
D. cuspidatum	TU440.1	syntypes *Leptoclinides cuspidatus*
	TU440.2	syntypes *Leptoclinides cuspidatus*
D. dealbatum	TU441.1	syntypes *Didemnum dealbatum*
	TU441.2	*Trididemum miniatum*
D. digestum	TU442.1	*Didemnum multispirale* sp. nov.
	TU442.2	paralectotype *Didemnum digestum*
D. dispersum	TU443.1	syntypes *Trididemnum dispersum*
	TU443.2	syntypes *Trididemnum dispersum*
D. elongatum	TU444	syntypes *Didemnum elongatum*
	TU445	syntypes *Didemnum elongatum*
D. fragile	TU446.1A	?*Didemnum precocinum* sp. nov.
	TU446.1B	syntypes *Didemnum fragile*
	TU446.2	?*Didemnum recurvatum*
D. fucatus	TU448	syntypes *Didemnum fucatum*
D. jedanense	TU454.1	lectotype *Didemnum jedanense*
	TU454.2	*Didemnum perplexum* sp. nov.
	TU454.3	*Didemnum multispirale* sp. nov.
D. makropnous	TU461.2	*Didemnum perplexum* sp. nov.
	TU461.3	*Didemnum grande*
	TU461.4	*Didemnum grande*
	TU461.5	*Didemnum grande*
	TU461.6	*Didemnum stragulum* sp. nov.
D. membranaceum	TU471.1	lectotype *Didemnum membranaceum*
	TU471.2	*Didemnum clavum* sp. nov.
D. ramosum	TU1271	paralectotype *Trididemnum sibogae* (nom. nov. for *Didemnum ramosum*)
	TU476.1	?
	TU476.2	*Trididemnum pigmentatum* sp. nov.
	TU476.3	lectotype *Trididemnum sibogae*
D. reticulatum	TU475.1	*Leptoclinides rufus*
	TU475.2	*Leptoclinides rufus*
	TU475.3	*Leptoclinides marmoratus*
	TU475.4	lectotype *Didemnum reticulatum* <*D. jedanense*
	TU475.5	paralectotype *Didemnum reticulatum* <*D. jedanense*
	TU475.6	*Didemnum caesium*
	TU475.7	*Leptoclinides rufus*
	TU475.8	*Didemnum caesium*
	TU475.9	*Leptoclinides cuspidatus*
D. tabulatum	TU480.1	syntypes *Didemnum tabulatum*
	TU480.2	syntypes *Didemnum tabulatum*
	TU480.3	syntypes *Didemnum tabulatum*
D. timorensis	TU1274 + TU482	holotype *Lissoclinum timorense*

resemble some of *D. ossium* and *D. astrum* although others with flat-tipped and rounded rays are lacking in the present species. It also has more larval ampullae than *D. astrum*, and although *D. ossium* does have a similar larva it has posterior abdominal cavities and more complex yellowish colonies than the thin red sheets of the present species.

Didemnum macrospiculatum Tokioka, 1967 from Kirabati is a pale, greyish colour with spicules (to 0.11mm in diameter) crowded in the surface and bottom layers of test. These spicules have very numerous conical rays, but globular spicules (as in *D. chartaceum*) do not occur. Most other species with such large spicules (e.g. *D. caesium*, *D. elongatum*) do not have so many rays.

Didemnum megasterix Monniot, 1995 (part: specimen from the south) from New Caledonia has spicules to about 0.1mm diameter, with 7–9 sturdy pointed conical rays in optical transverse section and about 10 larval ectodermal ampullae per side. Spicules are like those of *D. caesium* (>*D. megasterix* Monniot, 1995, part, specimen from the north) although the larvae are larger and have a blastozooid. *D. nocturnum* Monniot, F. & Monniot, C., 1997 has a similar larva but smaller spicules.

Didemnum nigricans Monniot, 1995 from New Caledonia has crowded spicules to about 0.045mm diameter. Its small zooids and surface test become brown after fixation like *D. albopunctatum* and *D. fuscum*, but the spicules have markedly conical rays that distinguish it. Its spicules are similar to *D. perplexum* but it has more (9) vas deferens coils and 5 rather than 6 pairs of larval epidermal ampullae.

Didemnum nocturnum Monniot, F. & Monniot, C., 1997 from Tanzania, is a deep blue in life (lighter patches where spicules are more crowded) and is brown in preservative. Zooids are in clumps surrounded by deep primary common cloacal canals. They have 6 or 9 (figs 6c, and 6d, respectively: Monniot, F. & Monniot, C., 1997) coils of the vas deferens and 10 stigmata in the anterior row. Spicules are stellate to 0.04mm diameter with 9–11 sturdy conical rays in optical transverse section. The larval trunk is 1.0mm long and has 8 or 9 lateral ampullae per side and a blastozooid. The maximum spicule size recorded is smaller than is usual for *D. caesium* although they are of similar form, as are the zooids and the colony (including its pigmentation). Larvae are larger in the present species and have a blastozooid — not reported in *D. caesium*. The present species has larvae like those of *D. megasterix* Monniot, 1995 (part, specimens from the south) but slightly larger, and the maximum spicule diameter is much less than the latter species.

Didemnum paa Monniot & Monniot, 1987 forms thin, white, pale-rose or yellow plates. Spicules (to 0.055mm diameter with 11–13 short conical points in optical transverse section) are crowded throughout. Spicules resemble those of *D. mutabile* Monniot & Monniot, 1987, from which *D. paa* is distinguished by its large number (10) of vas deferens coils and more numerous spicule rays (see also Monniot, 1995).

Didemnum parau Monniot & Monniot, 1987 from French Polynesia and the Phillipines (newly recorded colony QM G302912) forms thin, fragile, white colonies. Spicules (to 0.03mm diameter) are present throughout and have narrow, rod-like rays like those of *D. albopunctatum* and *D. fragile*. The post-pyloric part of the gut loop is flexed to form a double loop, the vas deferens coils 7 times, and the larval trunk is 0.37mm long with 4 lateral ampullae on each side. *D. fragile* has a brittle sheet-like colony, larger larvae (the larval trunk being about 0.45–0.5mm long), slightly larger spicules, and only 6 vas deferens coils. *D. albopunctatum* has more vas deferens coils.

Didemnum perlucidum: Monniot & Monniot, 1987 from French Polynesia and New Caledonia (Monniot, 1995) was assigned to the Atlantic Ocean species, *D. perlucidum* Monniot, 1983. Specimens from New Caledonia have 7 or 8 (?) coils of the vas deferens and small spicules (to 0.03mm diameter) with 5–7 conical rays in optical transverse section. The larval trunk is 0.45mm long, the same length as the nominal Atlantic species, but it is much less spherical and its tail is wound only two-thirds of the way around it (rather than completely encircling it). The species are most likely distinct from one another. The Pacific Ocean specimens resemble *D. perplexum* in the number of coils of the vas deferens and in the number of spicule rays but it differs in having only 4 pairs of larval epidermal ampullae (rather than 6 pairs) and smaller spicules. Its small spicules are a similar size to those of *D. granulatum* but it has fewer and possibly shorter spicule rays. However, the spicules of the western Pacific material have not been adequately described.

Didemnum pitipiri Monniot & Monniot, 1987 and Monniot, 1995 forms pale yellow encrusting colonies. The species has few unique characters. The spicules (to 0.03mm diameter) resemble *D. mutabile*, most having numerous (15–17) short conical rays and some having longer almost fusiform ones. The small larval trunk (0.33mm long) with 2 adhesive organs (from the type specimen) and the occasional larger spicules with fewer, larger rays, distinguish the species. *D. maculosum* from the north eastern Atlantic (see *D. candidum*, Remarks below), *Didemnum albopunctatum*, some *D. parancium* and *D. poecilomorpha* have only 2 adhesive organs, but are distinguished from the present species by many characters. *D. linguiferum* Monniot, 1985 has spicules of similar form to *D. pitipiri* but they are larger (to 0.08mm diameter).

Didemnum recurvatum Sluiter, 1909 (holotype ZMA TU474; Millar, 1975; *Polysyncraton recurvatum*: Kott, 1981) and *Didemnum* sp. (part, *D. fragilis* Sluiter, ZMA TU446.2) both from Indonesia, have hard cushion to sheet-like colonies, globular spicules to 0.03mm diameter, horizontal thoracic cloacal spaces, a retractor muscle from halfway down the oesophagus, about 8 stigmata per row, 5 coils of the vas deferens around 2 testis follicles, the post pyloric part of the gut loop bent at right angles and slightly twisted to the right and a large (about 0.8mm long) trunk with 4 pairs of lateral ampullae. Kott (1981) reported *D. recurvatum* to have been a distinctive dirty brownish colour in preservative owing to pigment cells in the surface. *D. bimasculum* Monniot, 1995 and *D. rubeum* Monniot & Monniot, 1996 also have a 2-lobed testis but they have symbiotic plant cells. Other forms with 2 male follicles

described from the western Pacific are *D. uturoa* Monniot & Monniot, 1987, *D. candidum*: Tokioka, 1967 (from Kiribati) and *D. bisectatum*, all readily distinguished by their spicules (see *D. fragile*, Remarks below). *D. precocinum* has smaller zooids, similar but larger spicules, undivided testis and a larval blastozooid and it lacks the pigmentation of the present species.

Didemnum rubeum Monniot & Monniot, 1996 from Chuuk Atoll and Palau Is has bright red to pinkish encrusting sheet-like colonies with globular spicules, 2-lobed testes, and large larvae and is reported to have symbiotic algae in the surface test and colonies that become green in preservative. It resembes *D. recurvatum* although symbiotic cells have not been reported in that species. *D.bimasculum* Monniot, 1995 has symbiotic cells and a 2-lobed testis, but has large stellate spicules to 0.1mm diameter. *D. viride* also is green in preservative, but lacks the globular spicules and 2-lobed testis.

Didemnum stercoratum Monniot & Monniot, 1996 from the Philippines forms soft, thin encrusting sheets, tan or yellow in life and white in preservative. The surface is marked into polygonal areas by depressions over the primary cloacal canals which have zooids along each side. Secondary cloacal cavities penetrate in amongst the clumped zooids surrounded by the primary canals. The 7 coils of the vas deferens and spicules (to 0.04mm diameter) are similar to those of *D. jedanense*, from which this species is distinguished by its lack of pigment, smaller larvae without blastozooids and smaller zooids. The species is one of the few reported to have faecal pellets in the basal test (see *Trididemnum savignii*).

Didemnum toafene Monniot & Monniot, 1987 from French Polynesia and New Caledonia (Monniot, 1995) has irregular, thin encrusting colonies. Spicules are crowded throughout. They are reported to 0.05mm diameter with 7–9 blunt conical rays in optical transverse section. Large spicules to (at least?) 0.08mm diameter with pointed rays of variable lengths are present, although the maximum diameter of these large spicules is not recorded. Zooids are less than 1mm long, 6 stigmata are in the anterior row, the retractor muscle projects from halfway down the oesophageal neck, 11 coils of the vas deferens surround the testis, and the larval trunk is 0.3mm long with 4 pairs of epidermal ampullae. The thin hard colonies resemble those of *D. inveteratum* sp. nov. but the zooids lack the atrial tongue of the latter species, and have more vas deferens coils, fewer spicule rays and generally smaller spicules. The larger spicules have more numerous rays than the tetrahedral giant spicules of *D. membranaceum*.

Didemnum albopunctatum Sluiter, 1909 (Figs 69, 165H; Pl. 7A,B)

Didemnum albopunctatum Sluiter, 1909: 58 (part, specimens from Ambon anchorage statn 231 only). Kott, 1981: 162.
Didemnum biglutinum Monniot, 1995: 300. Monniot & Monniot, 1996: 152.

NEW RECORDS. Queensland (Capricorn Group QM G308031-2 G308172; ? Swain Reefs, QM G308372; Whitsunday Is, QM GH5367).

PREVIOUSLY RECORDED. Indonesia (Ambon – ZMA TU433.2 lectotype Sluiter, 1909). Fiji (Kott, 1981). New Caledonia (Monniot, 1995). Palau Is (Monniot & Monniot, 1996).

COLONY. Colonies are firm, flat encrusting sheets, irregular in outline, with rounded borders and only 2–3mm thick. The surface always is smooth, with a thin bladder cell layer superficially and beneath that the small white calcareous spicules are crowded throughout the test — in the basal test, and in the sheaths of test associated with the zooids as they cross the cloacal cavities. The branchial apertures sometimes appear as dimples in the surface of the colony, and sometimes a clump of spicules is seen in the siphon.

Spicules are small (to 0.03mm diameter), relatively uniform, burr-like with crowded, flat- or round-tipped, long, narrow rod-like rays. The common cloacal cavity surrounds the thorax of each zooid with its narrow ventral sheath of test that connects surface to basal test. Abdomina remain in clumps, each clump surrounded by deeper cloacal cavities that extend the whole length of the zooids, or they are embedded in the basal test. Large common cloacal apertures are randomly distributed over the surface. Sometimes radial ridges crowded with spicules are in the roof of the cloacal cavity around each opening.

In preservative the colonies are beige to white, with brown pigment in the superficial bladder cell layer, colourless thoraces and yellow to white abdomina. In life, however, they were magenta[R] (QM G308172) or black-grey[R] (QM GH5367), with spherical red pigment cells in the superficial bladder cell layer, and red zooids. Type colonies and those recorded from Fiji (Kott, 1981) are said to have been dark to purple in life, although colonies from Palau were a greenish colour (Monniot & Monniot, 1996) and those from New Caledonia were brown (Monniot, 1995).

ZOOIDS. Zooids are small (barely more than 1mm), with a short branchial siphon and 6 well-formed rounded lobes around the aperture. The specimen (QM G308372) from the Swain Reefs has black squamous epithelum in the body wall of both thorax and abdomen, especially conspicuous around the anterior end of the zooid. The atrial aperture is large and open, exposing the whole dorsal surface of the branchial sac to the cloacal cavity, and it has a small anterior atrial lip which is inserted into the surface test and often is torn when the zooid is removed. Eight stigmata are in the 2 anterior rows, 7 are in the third row,

and 6 are in the posterior row. A short and thick to long and fine retractor muscle extends from the anterior part of the oesophagus out into the abdominal test sheath or basal test. The gut is long, the distal part of the loop bent up into a secondary loop. Nine spirals of the vas deferens surround the outer surface of the hemispherical testis. Larvae are present in the basal test of a colony (QM G308172) collected in March from the Capricorn Group. The tail curves a little more than three-quarters of the way around the trunk which is 0.5mm long. Four lateral ampullae, are along each side of only 2 median adhesive organs in the fully developed larva.

REMARKS. Preserved specimens assigned by Sluiter to this species have brown pigment in spherical to oval cells in the superficial test as reported for some of the newly recorded specimens. Spicules are not present in the test around the rims of the numerous sessile common cloacal openings. However, the spicules in each of Sluiter's specimens are different. The one that conforms with the species description (ZMA TU433.2) is proposed as the lectotype. Different species are represented by each of the other specimens (see Table 3).

Sluiter (1909) described the spicules of the present species as being spherical (up to 0.043mm diameter) with radially arranged needle-like rays terminating in small points. Although some of the spicule rays of the present species have irregular tips and are not strictly flat-ended, the majority of them are. The pointed rays that Sluiter reports are in specimens inadvertently assigned to the species — viz. ZMA TU433.1 (*D. perplexum*), TU433.3 (part, *D. multispirale)*, TU433.3 (part, *D. jedanense*) and TU433.4 (*D. jedanense*).

Didemnum fragile is a closely related species that lacks the dark pigment, has only 6 coils of the vas deferens and larvae with 3 (rather than 2) adhesive organs and shorter tails. The present species has spicules that resemble those of *D. precocinum* from which it is distinguished by its thin bladder cell layer, dark pigment in the test, hemispherical testis with 9 coils of the vas deferens and its larvae. *D. dealbatum* Sluiter, 1909 has spicules the same size and shape as the present species, but they are not present in the middle gelatinous layer of test. *D. hiopaa* has similar spicules and similar zooids with the same number of vas deferens coils, but its colonies are small, the test is soft and transparent and the spicules are only sparsely distributed.

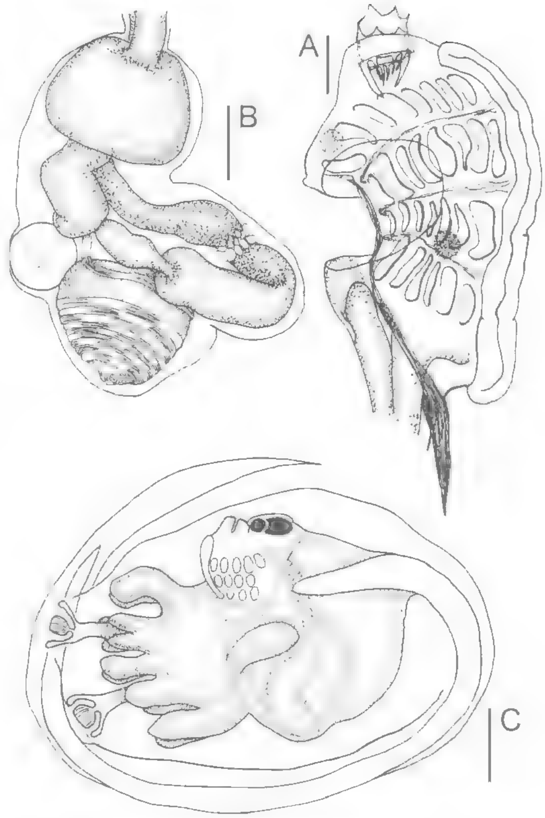


FIG. 69. *Didemnum albopunctatum* (A, QM G308032; B,C, QM G308172) – A, thorax; B, abdomen; C, larva. Scales: 0.1mm.

Didemnum biglutinum Monniot, 1995 from New Caledonia and the Palau Is (Monniot & Monniot, 1996) has the same gelatinous surface layer of bladder cells over a layer of brown pigment mixed with spherical black particles, small burr-like spicules crowded in the remainder of the test, and clumps of zooids surrounded by deep common cloacal canals, as Sluiter (1909) recorded for the type material. The larva, like the present species, has only 2 adhesive organs, 4 sets of lateral ampullae and a long tail; and the zooid has a similar number of vas deferens coils. This species and *D. albopunctatum* appear to be synonymous.

The black squamous epithelium in the body wall of the light grey specimen from the Swain Reefs (QM G308372) has not been reported previously in this species. Otherwise the specimen resembles others assigned to the present species. Dark squamous epithelium occurs commonly in *Diplosoma* and *Trididemnum* (see Glossary).

Didemnum arancium sp. nov.
(Figs 70, 166F; Pl. 7C,D)

Didemnum ligulum: Monniot & Monniot, 1987: 34 (part, orange colonies from French Polynesia).

TYPE LOCALITY. Queensland (Wistari Reef, low tide rubble fauna, coll. P. Kott 4.3.93, holotype QM G308115; Heron I., eastern end, rubble fauna, coll. P. Kott 9.3.93, paratype QM G308120).

FURTHER RECORDS. Queensland (Heron I., QM G308096, G308127, G308144, G308210, G308218, G308223, G308260, G308317, G308334; Swain Reefs, G305374, G308435-7).

PREVIOUSLY RECORDED. French Polynesia (Monniot & Monniot, 1987).

COLONY. Thin, sheet-like encrusting colonies have a hard, smooth surface, interrupted sometimes by slightly protuberant branchial apertures, with rows of spicules around the margins of the stellate openings. Spicules are only moderately crowded in the middle layer of test but are crowded in a basal layer of the colony and in a thin surface layer which is raspy to the touch. There is no spicule-free superficial layer of bladder cells. The cloacal cavity is thoracic, each thorax crossing it in association with a ventral sheath of test that joins the surface test to the basal test in which abdomina are embedded. Large, sessile common cloacal apertures randomly distributed over the surface lack spicules around the rims.

Most spicules are burr-like with numerous (to 21) long, rod- or needle-like rays with flat to chisel-shaped tips. Others have more numerous (up to 27 in optical transverse section) very short conical rays set in concavities in the central mass of the spicule. The latter are sometimes quite rare. Both types are up to 0.05mm in diameter and very occasionally to 0.07mm, but are more often in the vicinity of 0.02–0.04mm.

In life, colonies are salmon coloured[R], or buff pink[R] (a yellow colour), or orange-rufus[R], or orange vermilion[R] to saturn red[R] (a deep orange colour). Zooids are orpiment-orange[R] or scarlet vermilion[R], and larvae being incubated in the test are orange-chrome[R]. Orange zooids are often visible through the thin layer of surface test, and the colonies look spotted. In preservative colonies are apricot with bright orange zooids at first, but they fade to white, with yellow to yellow-beige zooids sometimes with a greenish gut and often some yellowish pigment in the basal test. *Prochloron* sometimes is on the surface, and in branchial siphons.

ZOOIDS. Zooids are moderately large, the extended thorax and abdomen together being about 1.3mm. The rim of the branchial aperture is divided into 6 triangular lobes. An atrial tongue, of variable length, extends from the anterior rim of the opening and usually is bifid at the tip. Often this is torn off as the zooid is removed from the test. The atrial aperture is wide, exposing most of the pharynx directly to the cloacal cavity. Eight stigmata are in the first 3 rows of stigmata, and 6 are in the posterior row. They are long and rounded at each end.

The gut loop is open, its ascending limb bent ventrally behind the testis, which is large and oval or dome-shaped with the vas deferens spiralling 7 times around its outer half. The long, thin retractor muscle is free from the anterior part of the oesophagus.

Embryos are being incubated in the basal test of both holotype and paratype. The larval trunk is 0.6mm long with the tail wound three quarters of the distance around the trunk. Ten lateral ampullae are on each side of the antero-median row of 3 adhesive organs. An oozooid with 7 stigmata in each of 3 rows and one blastozooid with 4 rows of stigmata are in the trunk.

REMARKS. The long atrial tongue, the numerous larval lateral ampullae, and the larval blastozooid also occur in *D. chartaceum*, *D. levitas* , *D. jedanense* and *D. precocinum*, from which the present species is distinguished by its spicules and by colony colour. *D. caesium* and *D. multispirale* which have a similar number of larval ectodermal ampullae (although a blastozooid may not be present), also are distinguished by their spicules. The atrial tongue, large number of larval lateral ampullae and larval blastozooids are reminiscent of, but do not necessarily indicate affinity with *Polysyncraton*.

Didemnum ligulum: Monniot & Monniot, 1987 apparently consists of 2 separate species, distinguished by differences in colony form and spicules. Neither of these species can be assigned to *D. ligulum* Monniot, 1983 from Guadeloupe which has significantly larger larvae (more than 0.8mm long) with more lateral ampullae, fewer stigmata, larger spicules with numerous but not crowded conical rays (like some from *D. multispirale*), and 6 coils of the vas deferens. The only thing that all the colonies assigned to *D. ligulum*: Monniot & Monniot, 1987 have in common with *D. ligulum* Monniot, 1983 is a forked atrial tongue (like, *D. albopunctatum*, *D. caesium*, *D. chartaceum*, *D. multispirale*, and *D. ossium*). *D. ligulum*: Monniot, 1995 from New Caledonia also is a different species from either

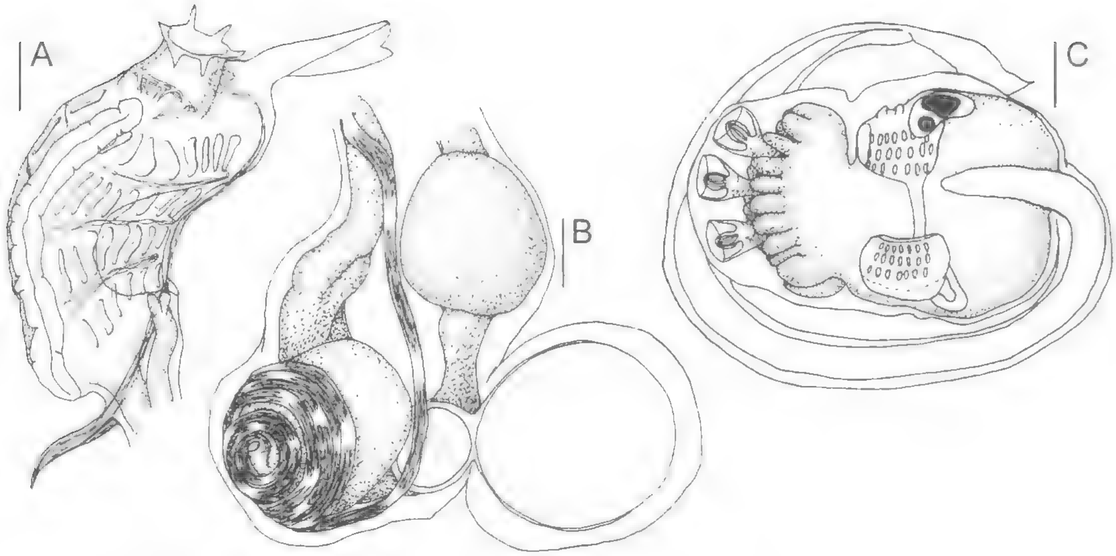


FIG. 70. *Didemnum arancium* sp. nov. (A, QM G308096; B,C, QM G308115) – A, thorax; B, abdomen showing gonads and gut loop; C, larva with thoracic blastozooid. Scales: 0.1mm.

the present one or the rose-coloured flat colonies from French Polynesia (assigned to the same nominal species; see *Didemnum ossium*). The thicker orange colonies from French Polynesia (Monniot & Monniot, 1987) are the same colour as, and appear to be conspecific with the present species, although larvae have a slightly shorter trunk (0.5mm long) than the newly recorded Australian ones.

Didemnum astrum sp. nov.
(Figs 71, 167F; Pl. 7E)

TYPE LOCALITY. Queensland (Wistari Reef, south side, low tide rubble fauna, coll. P. Kott 11.3.93, holotype QM G308015; Heron I, eastern end, lowtide rubble fauna, coll. P. Kott 4.9.94, paratype QM G308204).

FURTHER RECORDS. Western Australia (off Cape Preston, WAM 1.95). Queensland (Heron I. east, QM G300912, G308112, G308130, G308136, G308142, G308145, G308199, G308206, G308245, G308477; Swain Reefs, QM G305409, G308362). Indian Ocean (Cocos Keeling, WAM 605.89).

COLONY. Colonies are thin, hard but not brittle, small circular plates or sheets to more fleshy, robust encrusting sheets with rounded margins. The stellate branchial apertures usually (but not always) have spicules outlining them. Yellow or orange-yellow pigment cells are mixed with spicules and bladder cells in the superficial layer of the test. Zooids are scarlet^{R} or coral-red^{R}, and can be seen through the surface of the colony. One specimen (QM G308130) is reported to have been an even orpiment orange^{R} with orange zooids and another (QM G308362) was orange chrome^{R} with orange zooids. Only one colony is said to have been flame scarlet^{R} with ferruginous^{R} zooids obscured by the spicules in the surface layer. Preserved colonies usually are pale apricot, fading to white with a trace of yellow in the surface and/or basal test. The preservative often is a clear lemon colour.

Spicules are crowded beneath a surface bladder cell layer and around the zooids and sometimes are only moderately crowded to relatively sparse in the basal half of the colony. Most spicules (to 0.06mm diameter) have 11–13 pointed conical rays in optical section. Some smaller ones have short rounded or flat-tipped rays or are globular, and occasionally have longer almost fusiform rays. Bases of the spicule rays usually are crowded together. The cloacal cavity is thoracic, with the colony firm and robust as a result. However, deeper primary canals are present around clumps of zooids resulting in slightly protuberant oval surface swellings surrounded by narrow depressions over the deep primary cloacal canals. When contracted, margins of the common cloacal apertures often are frilled and translucent, but when open the rims are white with crowded spicules and lack pigment. One colony (QM G308477) has large protuberant lips around the common cloacal apertures.

ZOOIDS. Zooids are small, about 0.7mm long when contracted. The branchial siphon is well-formed and cup shaped, with 6 sharply

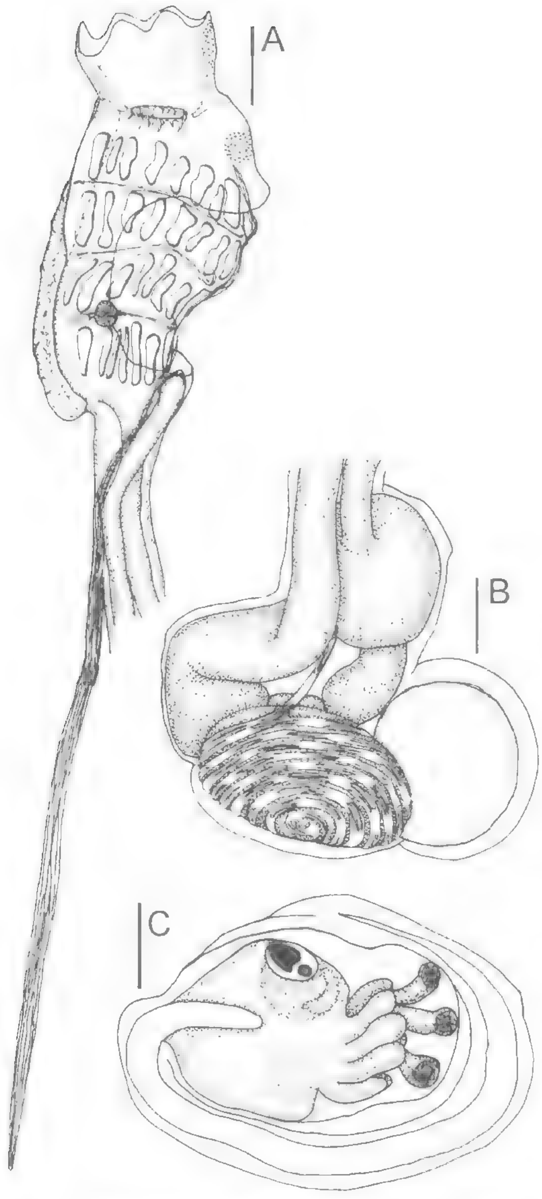


FIG. 71. *Didemnum astrum* sp. nov. (A, QM G308204; B,C, QM G308245) – A, thorax; B, gonads and gut loop; C, larva. Scales: 0.1mm.

pointed lobes around the rim of the lobes. An atrial lip was not detected. The branchial sac has 8 stigmata in the anterior rows and about 6 in the posterior row. The long, strong retractor muscle is free from about halfway down the long oesophagus. The testis has 10 coils of the vas deferens around its outer half.

Larvae are in colonies collected in March (QM G308112) and October (QM G308245) . The small trunk (0.35mm long) has 4 large lateral ampullae along each side of the 3 antero-median adhesive organs.

REMARKS. The species is distinguished by the crowded, regular, pointed, conical rays of the majority of its spicules. The long, robust retractor muscle from halfway down a relatively long oesophageal neck is also a characteristic of this species. Spicules resemble, but are smaller and have fewer and longer rays than in *D. chartaceum*. *D. lacertosum* has only slightly smaller but less diverse spicules with more rays. The spicules are similar to *D. multispirale*, although in the latter species the rays are shorter and separated from one another on the central spicule mass rather than having their bases crowded together. Spicules of *D. moseleyi* show the same diversity as those of the present species, but they have fewer rays.

D. mutabile, *D. paa* and *D. pitipiri* from French Polynesia (Monniot & Monniot, 1987) have spicules with equally numerous, but invariably shorter rays separated from one another on the spherical central mass as in *D. multispirale*.

The small rose-coloured specimens of *D. ligulum*: Monniot & Monniot, 1987 from French Polynesia have similar characters to the present species, viz. small circular colonies, and some spicules with numerous pointed rays while others have round-tipped rays (see Monniot & Monniot, 1987: pl. 2C). However, their larvae are different — a blastozooid was not detected, and they have only 4 pairs of ectodermal ampullae – and the cloacal systems are different.

Didemnum bicolor sp. nov.
(Figs 72, 168G; Pl. 7F,H)

TYPE LOCALITY. South Australia (Investigator Group, Top Gallant I. in caves, coll. N. Holmes 10.4.83, holotype QM GH2410; Ward I. in caves, 8m, coll. N. Holmes 14.4.83, paratype QM GH2409.

COLONY. Colonies are hard, irregular, encrusting sheets to 5mm thick, with black pigment in the surface contrasting with white pigment-free areas, creating a black and white marbled pattern in the surface, like a piebald horse. The pattern varies, sometimes white predominates but other parts of the surface and other colonies are almost entirely black with white only around the common cloacal apertures. Some elongate or oval areas of test are zooid free, and project slightly from the surface and zooids

are partially embedded along each side of the deep primary common cloacal canals that surround these areas. These primary canals are almost the full depth of the colony, and the test over them is slightly depressed in preserved colonies. However, zooids are not always confined to the primary canals, and in some places occur in clumps with shallow secondary common cloacal spaces penetrating amongst them at thorax level. Zooids open in both pigmented and unpigmented areas, their arrangement not being associated with the colour pattern. The colour pattern is present in preserved as well as in living specimens.

Spicules are present throughout, although they are most crowded in the hard opaque lower half of the colony. They are small, to 0.03mm diameter. Generally they have 11–13 conical pointed or truncated flat-tipped rays in optical transverse section, but occasionally there are spicules with fewer rays (9) or more (15) and one larger spicule (0.04mm diameter) was detected.

ZOOIDS. Zooids are relatively large, to about 3mm long. The thorax is almost rectangular, with a conspicuous tulip-shaped branchial siphon, a wide open atrial aperture exposing most of the branchial sac, and a bifid atrial lip from the anterior rim of the opening. This atrial lip is of variable size but usually is narrow. The branchial siphon is difficult to remove from the test, having a plug of tightly packed spicules in its test lining. A long tapering retractor projects from about halfway down the oesophageal neck, and a large lateral organ is on each side of the thorax. Eight stigmata are in the anterior row, and only in the last (fourth) row is the number reduced to 6.

The abdomen is relatively short and the gut loop gently curved. Gonads are not developed in either holotype or paratype. Some zooids have small thoracic buds in the oesophageal region.

REMARKS. Spicules with pointed and truncated rays, large thorax and conspicuous black and white colour pattern characterise the species.

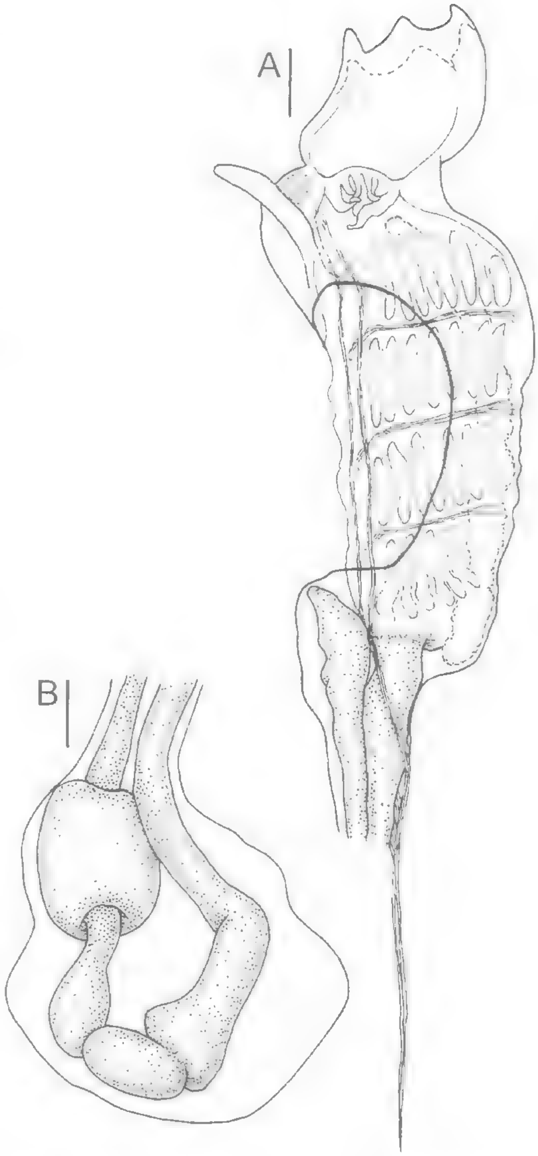


FIG. 72. *Didemnum bicolor* sp. nov. (QM GH2410) – A, thorax; B, gut loop. Scales: 0.1mm.

The thoraces with their large tulip-shaped branchial siphons, wide open atrial apertures and narrow atrial lips are like those of *D. ossium.* The latter species also has blunt-tipped spicule rays as well as those with pointed rays, but the rays are longer with sharper points than those of the present species, the spicule diameter is greater and the common cloacal systems are different from the present temperate species. *D. jucundum* also has a black colony but its spicules are much larger and have more numerous rays. Species with a similar mixture of conical pointed and flat-tipped truncated rays are *D. inveteratum* which has more numerous spicule rays and larger spicules; and *D. apuroto* Monniot & Monniot, 1987 from French Polynesia and *D. diffundum* Monniot, 1995 from New Caledonia, which have spicules with fewer rays (7 to 9 and 9 to 11, respectively) than the present species and different colonies. Similar spicules occur in *Polysyncraton millepore.*

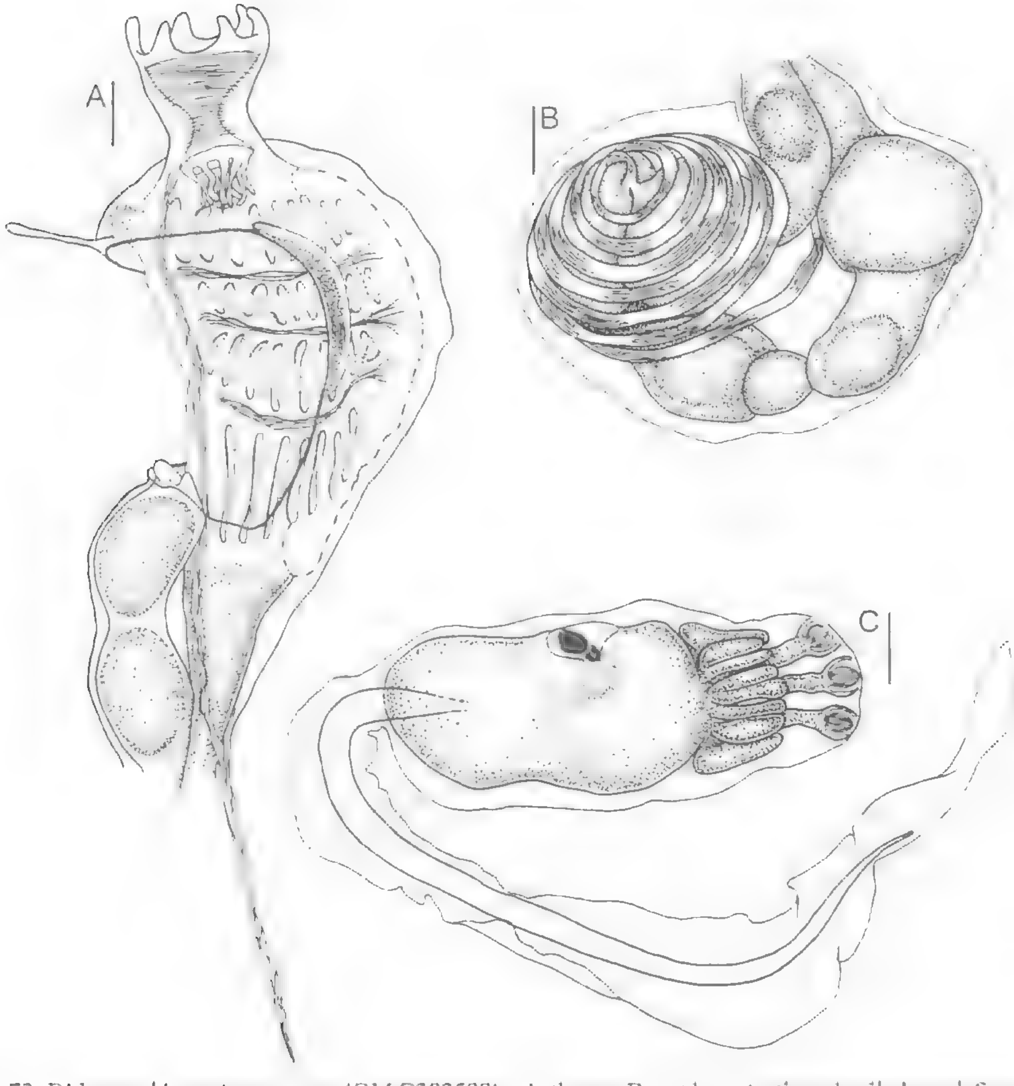


FIG. 73. *Didemnum bisectatum* sp. nov. (QM G302599) – A, thorax; B, gut loop, testis and coiled vas deferens; C, larva. Scales: 0.1mm.

Didemnum bisectatum sp. nov.
(Figs 73, 168F)

TYPE LOCALITY. Northern Territory (Flat Top Bank, Timor Sea 12°16'S, 129°15'E, coll. J.N.A. Hooper, holotype QM G302599).

COLONY. The hard, encrusting colony, about 3mm thick, has spicules crowded throughout. Some brownish pigment is mixed in the surface layer of test, but bladder cells were not detected. The common cloacal cavity is a shallow horizontal space at thorax level. Some plant cells are embedded in the surface test, and the preservative is stained greenish yellow. The spicules are relatively large to 0.07mm in diameter and most have 17–19 conical or flat-tipped truncated rays in optical transverse section. A few of the spicules are globular.

ZOOIDS. Zooids are robust with short funnel-shaped branchial siphons with 6 pointed branchial lobes. The atrial aperture is wide, exposing most of the branchial sac directly to the cloacal cavity. A delicate narrow atrial lip (usually with a rounded tip but sometimes forked) projects from the mid-dorsal body wall just anterior to the atrial aperture. The thorax is turnip-shaped, the posterior (post-stigmatal) part gradually tapering to the part of the oesophageal neck where the strong, tapering retractor muscle

projects into the test. The top of the oesophagus is wide — almost the same diameter as the posterior end of the thorax. The lateral organ is a shallow, long, narrow concavity stretched out between the middle of the first and third rows of stigmata in the antero-lateral part of the rim of the widely stretched atrial opening. Pointed, columnar epithelial cells project from the body wall especially conspicuous along the dorsal wall of the concavity of the lateral organ. Unusual columnar cells along dorsal wall of the concavity have a papillate appearance. The concavity tapers anteriorly. Nine long narrow stigmata are in the first and second rows of stigmata, reducing to 8 in the third and 7 in the posterior row. The gut loop is short and simple and the conical to lens-shaped testis, divided into 2 lobes, with 7 tight coils of the vas deferens around it, lies against the dorsum of the pole of the gut loop.

Larvae, with a trunk to 0.75mm long and the tail wound about three-quarters of the way around it are in the holotype. They have 4 subdividing ectodermal ampullae along each side of the 3 antero-median adhesive organs. Blastozooids are not present.

REMARKS. Other species of *Didemnum* known to have 2 testis lobes are *D. bimasculum* Monniot, 1995 from New Caledonia which also has similar larvae, long lateral organs and the same number of vas deferens coils, but has larger spicules with fewer rays; *D. uturoa* has unusual bilaterally symmetrical spicules; *D. recurvatum* Sluiter, 1909 with globular spicules lacks an atrial tongue; an undescribed species from SW Australia that Kott (1962) erroneously assigned to *D. augusti* (see *D. patulum* below) with spicules about 0.04mm diameter, about 10 pointed rays in optical transverse section and 6 coils of the vas deferens; and *D. candidum*: Tokioka, 1967 from Kiribati. *D. mutabile* has spicules of similar size but spicules with short truncated rays are not known, the testis is undivided and the larval trunk is only 0.3mm long, with 5 ectodermal ampullae per side. *D. grande*: Kott, 1962 from Rottnest I. (which was said to have 2-lobed testis) appears to be an immature colony of *Polysyncraton* sp. (see *P. palliolum*, Remarks).

Didemnum caesium Sluiter, 1909
(Figs 74, 170A)

Didemnum caesium Sluiter, 1909: 53.
Didemnum reticulatum Sluiter, 1909: 60 (part , specimens from statn 315 and statn 322).
Didemnum megasterix Monniot, 1995: 315 (part, specimens from the north).

NEW RECORDS. Western Australia (Montebello Is, WAM 960.93; off Port Hedland, WAM 513.92). Queensland (Capricorn Group, QM G300894, G301584, G302968, G308014, G308084-5, G308265, G308285, G308290, G308296).

PREVIOUSLY RECORDED. Indonesia (holotype ZMA TU434 Sluiter, 1909; *D. reticulatum* ZMA TU475.6, TU475.8 Sluiter, 1909). New Caledonia (Monniot, 1995).

COLONY. Colonies sometimes are thin but others are robust sheets to 5mm thick, more or less flat on the upper surface which is interrupted by large, cloacal apertures evenly spaced along elevated surface ridges. The superficial layer of test has black and brown pigment in narrow irregularly shaped cells mixed with white calcareous spicules over a layer of crowded spicules about 3 or 4 deep. A thin layer of spicules is on the base of the colony. Spicules are sparse in the remainder of the colony. Pigment cells are present in the test beneath the crowded layer of spicules, above the cloacal cavities. Cloacal spaces are oesophageal and sometimes posterior abdominal. Zooids lie more or less horizontally above the cloacal spaces with the ventral part of the thorax embedded in the surface test. Spicules often are absent around the branchial apertures, although some small groups of 2 or 3 are in the lining of some of the branchial siphons. Spicules are generally large (to 0.1mm in diameter), stellate, with 9–11 and occasionally 7 conical rays in optical transverse section with acutely pointed and sometimes chisel-shaped tips. Larger spicules predominate, but also there are some very much smaller ones in the 0.01–0.02mm diameter size range, some of which have club-shaped rays. Ray length/spicule diameter ratio is about 0.25–0.3.

In life, colonies are blue-black, or slate blue, or purple with black, with white patches around the cloacal apertures where pigment cells are absent from the test, exposing the white spicules. However, spicules are not present in the actual rims of the cloacal apertures. In preservative the colonies are purplish-brown or grey, with pale to white margins around the cloacal apertures, although the black pigment of the basal test is seen through the openings. *Prochloron* is present in patches on the surface of some of the colonies.

ZOOIDS. Zooids are robust, reaching about 2.0mm long when relaxed. They are blackish in preservative, with black pigment in the body wall although they fade to brown in longer term preservation. The thorax is relatively broad and there is a fine, tapering retractor muscle from about halfway down the oesophageal neck. Six

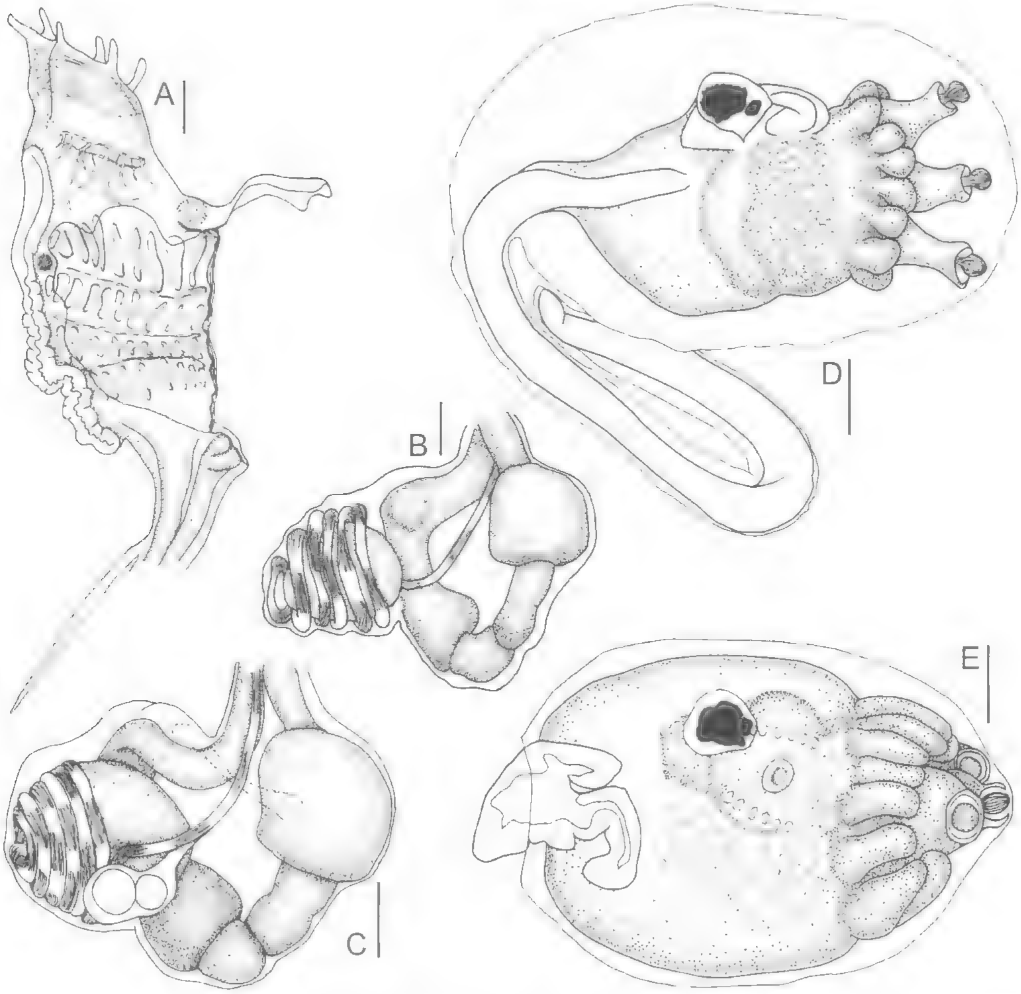


FIG. 74. *Didemnum caesium* (A,B, QM G302968; C, QM G308084; D,E, QM G308290) – A, thorax; B, abdomen; C, abdomen; larvae, D, from the right side, with tail beginning its withdrawal, and E, from above with tail being resorbed. Scales: 0.1mm.

narrow, pointed lobes surround the branchial aperture, which is on a short, wide cylindrical siphon. The large atrial aperture, which sometimes exposes the whole dorsal part of the branchial sac, has a strong, muscular, bifid atrial tongue, which is embedded in the test above the cloacal cavity and sometimes is torn off when the zooids are removed. A circular lateral organ is an each side of the endostyle between the first and second rows of stigmata. There are 10 stigmata in the anterior rows of the branchial sac, 9 in the third and 8 in the last row. The gut is thick and the post-pyloric part of the gut loop is bent ventrally up against the anterior part. The duodenum is relatively long, the posterior stomach short, the proximal part of the rectum very thick and wide and the distal part relatively narrow.

Sometimes a large, oval testis projects from the dorsal surface against the distal end of the gut loop. It has 6 coils of the vas deferens around its long axis, the proximal coil (from the outer tip of the oval) and the distal coil (against the gut loop itself) of smaller diameter than the coils around the middle (wider) part of the testis. However, in other specimens the testis is the usual conical shape. A large egg is dorsal or anterior to the male follicle.

Embryos are being incubated in the basal test of colonies collected in March (QM G308084-5), September (QM G308290) and October

(G308296). In one larva only 2 adhesive organs were found — although that could be abnormal, as 3 are in the embryos being incubated in the basal test of other specimens. The larval trunk is 0.65mm long and a long tail almost completely encircles it. On each side, 4 lateral ampullae subdivide to form the 16 that encircle the anterior end of the trunk in mature larvae. The trunk is thick, without any appreciable waist. Masses of yolk are present but a blastozooid was not detected. Generally adult organs are not well advanced in the known larvae and although the pharynx is perforated in some in which the tail is being resorbed, specimens with the tail entire and epidermal ampullae well developed do not always have a perforated pharynx.

Conspicuous small, oval clusters (about 0.01mm longest dimension) of minute spheres (0.002 diameter), which appear as dark dots at lower magnification, are embedded in the larval test around the base of the tail at the posterior end of the trunk of the more advanced larvae (QM G308290). The size of this mass of dark test inclusions increases as the larva matures, and although it is in the same position as the larval rastrum in *Diplosoma* symbioses (see *D. simile*, below) it is not a rastrum, the inclusions are not recognisable as symbionts and they may be test cells.

REMARKS. The species is distinguished by absence of spicules from the middle of the colony, large spicules with acutely pointed rays, darkly pigmented colonies, robust zooids with wide thoraces, distinct atrial tongues, short and wide branchial siphons, conspicuously pointed branchial lobes, anterior lateral organs, oval testis and an unusual larval trunk with numerous ectodermal ampullae but no blastozooid. The colony resembles *D. chartaceum* in the distribution of spicules, but the spicules are a different shape. *D. cuspidatum* Sluiter, 1909 has colonies that are said to have been grey-blue but re-examination of its syntypes (ZMA TU440.1, TU440.2) has shown that although the spicules are similar in size and form to those of the present species, the specimens belong to *Leptoclinides*. The unusual oval testis follicle projecting from the dorsal surface of the abdomen, occurs in *D. granulatum* and *D. fragile* and may be an artefact.

D. multispirale has similar larvae with numerous ectodermal ampullae and without blastozooids, but it lacks dark inclusions in the larvae and in the adult colony, and the spicules are different and crowded throughout.

D. grande has similar spicules although they are crowded throughout and their ray length/spicule diameter is greater. It has a distinct spicule-free pigmented bladder cell layer, zooids arranged in clumps surrounded by deep common cloacal canals marked by depressions in the surface, and only 4 pairs of larval lateral ampullae. *D. nocturnum* Monniot, F. & Monniot, C., 1997 from Tanzania has a similar colony and zooids to the present species. The spicules, though of the same form, are smaller and the larvae are longer and have a blastozooid.

Monniot (1995) has 2 different sorts of larvae in specimens assigned to *D. megasterix* Monniot, 1995 from New Caledonia, viz. specimens from the north which do not discolour in formalin have smaller larvae identical with the present species; and others from the south which do discolour in formalin have larvae about twice the size with more numerous ectodermal ampullae, blastozooids, and perforated oozooid and blastozooid pharynges. Larvae do not usually appreciably increase their size with development, and rather than being 2 different stages of development these larvae are from different species, the northern one the present species. Larvae of the southern forms are of the *Polysyncraton* type with a larval blastozooid and numerous lateral ampullae. They occur also in *D. arancium*, *D. chartaceum*, *D. jedanense*, *D. levitas* and *D. precocinum*, none of which have spicules like those of *D. megasterix* Monniot, 1995 (part, specimens from the south) which does not appear to occur in Australia.

Didemnum candidum Savigny, 1816
(Figs 75,171B,C; Pl. 8A,B)

Didemnum candidum Savigny, 1816: 194. Hartmeyer, 1915: 419. Michaelsen, 1919: 18 (part, specimens from Gulf of Suez): 1920: 19. Hastings, 1931: 94 (part, dredged specimens). Tokioka, 1967: 62 (part, not burr-shaped spicules). Eldredge, 1967: 213. Lafargue, 1974: 341 (part, fig. C). Kott, 1998: 81 (part, Indo-West Pacific tropical records only).

Not *Didemnum candidum*: Van Name, 1921: 323; 1930: 435; 1945: 83. Carlisle, 1954: 314. Tokioka, 1954: 246. Kott, 1962: 328; 1972a: 19; 1972b: 179; 1975: 9; 1976: 65. Millar, 1982: 49.

Leptoclinum cretaceum Sluiter, 1898: 36.

Didemnum yolky Monniot, C. & Monniot, F., 1997: 1627. Monniot, F. & Monniot, C., 1997: 10.

NEW RECORDS. Western Australia (Ashmore Reef Timor Sea, WAM 517.92; Kimberley, WAM 746.91). Queensland (Capricorn Group, QM G302995, G308002, G308029, G308040, G308045, G308047-8, G308111, G308113, G308125, G308129, G308183, G308186-7, G308189, G308202, G308215, G308222, G308225, G308248, G3308319, G308335; Swain Reefs, QM

G305557, G305700-2, G308370, G308391, G308399, G308410, G308430, G308438).

PREVIOUSLY RECORDED. Queensland (Hastings, 1931). Western Pacific (Tokioka, 1967). Gulf of Suez (Savigny, 1816; Hartmeyer, 1915; Michaelsen, 1919, 1920). Gulf of Arabia (Monniot, C. & Monniot, F., 1997). West Indian Ocean (Mozambique – Sluiter, 1898; Mauritius, Malagasy – Michaelsen, 1920; Tanzania – Monniot, F. & Monniot, C., 1997).

COLONY. Colonies are thin, irregular investing sheets Generally the surface is smooth but sometimes small spicule-filled papillae ornament it (QM G308189, G308319, WAM 74.91). Minute crowded papillae on the surface of the latter specimen sometimes join up with one another to form a sort of scaffolding on the surface, including a radial pattern around the stellate branchial apertures. Specimens are found on hard substrates or weed. They always are white in preservative, but in life they are either vinaceous[R], vinaceous red[R] to flesh colour[R], vinaceous rufus[R], ferruginous[R], brick red[R], flame scarlet[R], dragons-blood red[R], vermilion[R], orange vermilion[R], orange (saturn red[R]) or orpiment orange[R] and one specimen was rose pink[R]. The pigment is in minute spherical cells in the superficial layer of test over the white spicules which are crowded throughout the remainder of the test. Zooids usually are darker than the surface of the colony, and are scarlet[R], flame scarlet[R], crimson[R], claret brown[R], burnt carmine[R], vermilion[R], or bright orange (saturn red[R]). They can be seen through the surface of the colony, and sometimes appear as red or orange spots with a white dot in the centre where spicules in the lining of the branchial siphon line the stellate apertures or are crowded in the test around them. Occasionally spicules appear to form a plug in the branchial siphon. Common cloacal apertures appear white inside owing to the spicules crowded in the test, although the rim of the opening is red or orange in living specimen owing to the absence of spicules there. Preserved specimens are pale apricot at first with pale transparent beige zooids. However, soon they fade to white.

Extensive horizontal common cloacal spaces at thorax level have the thoraces crossing the space independently, each with a ventral test sheath that connects the surface to the basal test. The cloacal cavity sometimes extends deeper around groups of zooids, leaving clumps of abdomina projecting into the common cloacal cavity.

Spicules are of moderate size, with 7–9 rays in optical transverse section never exceeding 0.06mm in diameter, and usually being less than 0.05mm. Most have moderately long slightly club-shaped or cylindrical rod-like rays, rounded at the tip. A few have conical rays. Ray length/spicule diameter ratio is about 0.38. Spicules have a particularly large size range, many very small spicules being crowded in between larger ones. Spicules are not always evenly distributed in the surface layer of test, sometimes being crowded into clumps forming particularly opaque patches on the surface. Sometimes the surface of the colony has a sightly frothy appearance owing to the uneven distribution of spicules.

ZOOIDS. Zooids are small, about 1mm long. The relaxed thorax is about 0.5mm long. They have 6 well-formed, pointed branchial lobes. A wide open atrial aperture exposes a large part of the branchial sac directly to the cloacal cavity and a large thoracic organ is along the posterior part of the ventral rim of the aperture on each side. A retractor muscle of variable length is free from the middle part of the oesophageal neck. In the branchial sac are 6 stigmata in the first 2 rows, 5 in the third row and 4 in the last. Often thoraces are too contracted for stigmata to be counted accurately. Generally the thorax tapers slightly toward the posterior end. The stigmata are fusiform coming to a point at each end with 3 large, darkly staining, non-ciliated terminal cells at each end.

The gut loop is relatively long, and its distal tip is flexed ventrally. In sexually mature zooids a large testis is beneath this flexed part of the gut loop. The testis is hemispherical or a low dome. The inner side, or base of the testis (the part against the gut loop) is flattened. The vas deferens always spirals 7 times around the outer surface of the testis.

Larvae are present in newly recorded colonies taken in March (QM G308002, G308047-8, G308189) and September (QM G308202, G308410). Sometime they are found in the surface test, in the process of being liberated from the surface of the colony. The larval trunk is 0.3 (QM G308189, G308410) to 0.75mm long, with the usual ocellus and otolith, and 4 pairs of lateral ampullae along each side of the 3 antero-median adhesive organs. The tail is wound only about halfway around the trunk.

REMARKS. This species (the type of the genus) is one of the most commonly encountered *Didemnum* species in Australian waters. Its thin, brittle colonies, small spicules, small zooids and

variable colour (some shade of red or orange) are common in the genus. In the field it can readily be confused with *D. membranaceum*, *D. fragile*, as well as many other species. Its larvae also are similar to many other *Didemnum* spp.

The form of the spicules is the only unique character so far determined. Spicules with long pointed rays and giant spicules (as in *D. membranaceum*) do not occur. The spicule rays of *D. perplexum* are fewer, shorter and more conical than the present species, which has rod-like rays similar to those of *D. fuscum* but smaller. *D. fuscum* is further distinguished by its more numerous vas deferens coils, large dark spherical cells around the zooids and small larvae with more lateral ampullae. The only other character which helps to distinguish *D. candidum* from many others is the origin of the retractor muscle from halfway down the oesophageal neck, although that is by no means unique and is often obscured when zooids are contracted. Fusiform stigmata with pointed ends occur also in *D. perplexum*. *D. sphaericum* Tokioka, 1967 has similar spicules, but their rays are fewer, shorter and more conical. Specimens assigned to *D. sphaericum* from Fiji (Kott, 1981) have rays sometimes set in pentagonal bases.

Unfortunately the type specimen of *D. candidum*, from the Gulf of Suez, has not survived. Hartmeyer (1915) studied a number of specimens from the Gulf of Suez in the collection of the Berlin and Hamburg Museums that he considered to be conspecific with Savigny's species, and described them in some detail. He records encrusting, moderately thin, brittle sheets that are seldom more than 1mm thick, as well as cushions and more complex colonies folded back on themselves to form semi-enclosed spaces. He found the upper surface to be smooth, pierced by 6-lobed stellate branchial apertures. The spicules, crowded throughout, are of very constant form — stellate with 7–9 regular conical rays in optical section and up to 0.06mm in diameter. The rays are slightly blunt-tipped, although smaller spicules have more pointed rays. Zooids are scarcely 1mm long, with 8 stigmata per row in the branchial sac, and 5–6 coils of the vas deferens (Hartmeyer, 1915). He pointed out that the species was then known for certain only from the Gulf of Suez.

Carlisle (1954) found that specimens from the Gulf of Suez identified by Hartmeyer (preserved in The Laboratory, Plymouth) were characterised by having only 2 larval adhesive organs.

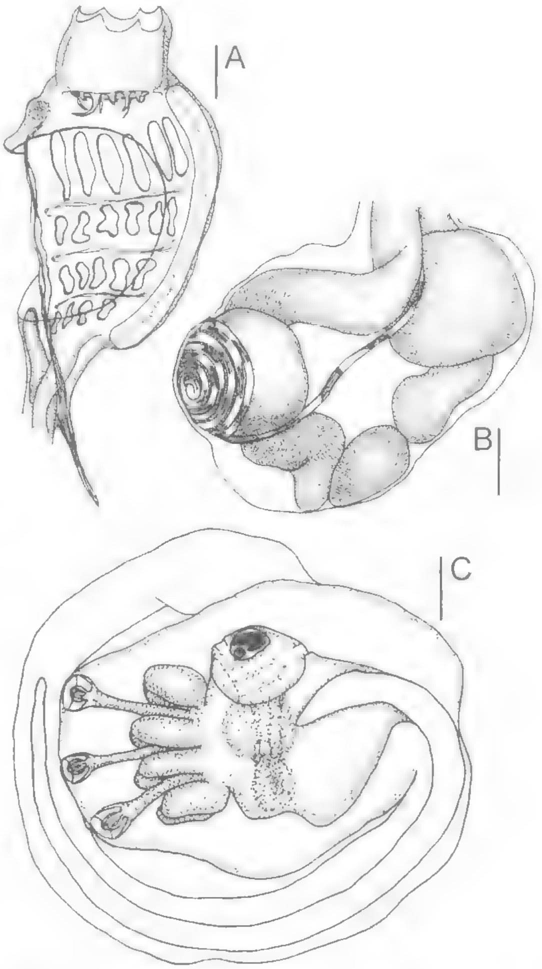


FIG. 75. *Didemnum candidum* (A, QM G308186; B, QM G308189; C, QM G308202) – A, thorax; B, abdomen; C, larva. Scales: 0.1mm.

However Lafargue (1972, 1974) found that all of the specimens she collected from the Red Sea had 3 (rather than 2) larval adhesive organs. It appears that Carlisle (1954), working with a mixture of species, confused European and Indo-Pacific specimens. Lafargue (1972, 1974) concluded that *D. candidum* Savigny, 1816 has an Indo-West Pacific range, and that it has 3 adhesive organs. Specimens assigned to the species from NW Europe, the Mediterranean and the northern Atlantic have only 2 adhesive organs and belong to *D. maculosum* (Milne Edwards, 1841).

Lafargue (1974) erected a neotype series from Eilat in the Gulf of Aquaba (near the type location, the Gulf of Suez). Unfortunately the spicules from this syntype series are unusually diverse and it is unlikely that they are from a

single species. Those illustrated in figure 2C (Lafargue, 1974) are similar to the spicules in the specimens referred to *D. candidum* in the present work, and to those described by Hartmeyer (1915). Lafargue's description of the zooids and colony otherwise conforms with Hartmeyer's (1915), except in regard to the number of stigmata per row, which Hartmeyer recorded as 8 — a relatively high number. *D. yolky* Monniot, C. & Monniot, F., 1997 from the Arabian Gulf, conforms in every way with *D. candidum*.

Synonymy of *Leptoclinum tenue* Herdman, 1886 (from the Magellanic region and the northern Atlantic) with the present species cannot be sustained, there being significant differences in spicule size and form (Michaelsen, 1919). Similarly there are significant, even dramatic differences in size, form and distribution of spicules of specimens from the tropical Atlantic proposed as synonyms by Van Name (1945). Differences of this magnitude cannot be considered intraspecific. Owing to Van Name's authority and usual reliability in this field, the proposition (that they are intraspecific) has obscured the taxonomic significance of certain characters and distorted the definition and affinities of this and other species in *Didemnum*, resulting in the assignation to this species of a bewildering number of specimens from a range of locations.

Specimens incorrectly assigned to *D. candidum* include many from temperate Australian waters with small, many rayed and sometimes globular spicules (Kott, 1972a, 1972b, 1975, 1976); and others from its known range in the Indo-West Pacific, which have different spicules (Hastings, 1931; Tokioka, 1954, 1955, 1967).

Tokioka (1967: 64) included, in the present species, specimens with 1–3 testis follicles, 4 or 5 to 8 or 9 coils of the vas deferens, maximum sized spicules 0.03–0.064mm diameter, either crowded or sparse throughout or sparse above individual zooids, with 6 –9 or more (up to 15) rays in optical transverse section. He concluded that 'The general structure of the zooids conforms well in detail with that of common didemnids'. This attempt at rationalisation reflects the confusion that has existed in this species and many others in the genus *Didemnum*.

Didemnum chartaceum Sluiter, 1909
(Figs 76, 166G; Pl. 7G)

Didemnum chartaceum Sluiter, 1909: 57. Hastings, 1931: 97. Kott, 1981: 163; 1998: 81.
Didemnum obscurum: Monniot, 1995: 319 (part: colonies from the barrier reef; ? colonies from the Seychelles). Monniot, C. & Monniot, F., 1997 p. 1626.
Not *Didemnum obscurum* Monniot, 1969: 453.
Didemnum nigrum Monniot & Monniot, 1996: 158.

NEW RECORDS. Queensland (Capricorn Group, QM G302966, G308005, G308007, G308054-6, G308067-9, G308073-5, G308267-9, G308299; Swain Reefs, QM G305618, G305682, G308266, G308383, G308397; Lihou Reef, QM G306993). Andaman Sea (Similan Is, QM G300950).

PREVIOUSLY RECORDED. Queensland (Low Is – BMNH 1930.12.17.45 Hastings, 1931). Indonesia (ZMA TU437 Sluiter, 1909). Philippines (Monniot & Monniot, 1996). Fiji (Kott, 1981). New Caledonia (Monniot, 1995). ?Seychelles (Monniot, 1995). Arabian Gulf (Monniot, C. & Monniot, F., 1997).

The newly recorded specimen QM G306993 is reported to have been from a large population on a hard, consolidated substrate on a high energy slope site on the seaward side of Lihou Reef.

COLONY. Colonies are dark fleshy, encrusting sheets with a single layer of spicules beneath a thick superficial layer of bladder cells. The common cloacal cavity is a horizontal space at the level of the thoraces. Zooids are embedded in the test with the ventrum against the spicule layer and the dorsum facing the cloacal cavity. Only occasional spicules are in the basal test beneath the cloacal cavity, although a thin layer is on the base on the colony. Bladder cells throughout the test give it a spongy consistency. Branchial apertures have spicules crowded in their linings, sometimes appearing to outline the stellate opening, but sometimes crowded in the test around the aperture. In life, the colonies are bay colour[R], claret-brown[R], heliotrope purple[R], mottled brown and mauve[R], dahlia purple[R], magenta[R] or black, depending on the concentrations of pigment in the surface. In one colony there is a light grey and dark grey reticular pattern in the surface caused by clumps of spicules mixed with pigment and bladder cells in the superficial test. The newly recorded colony from the Andaman Sea (QM G300950) is black. Occasionally *Prochloron* is on the surface test. Burnt carmine[R] to purplish-brown zooids are seen through the white spicule layer. Common cloacal apertures (about 5mm apart) have dark rims resulting from the absence of spicules, although 5 groups of spicules around the rim are continuous with the radial ribs in the roof of the cloacal cavity around the aperture. The basal test is a translucent plum colour. In preservative, colonies are purple-grey to brown, with dark purplish-brown zooids. The preservative stains brownish purple to yellowish-brown and the

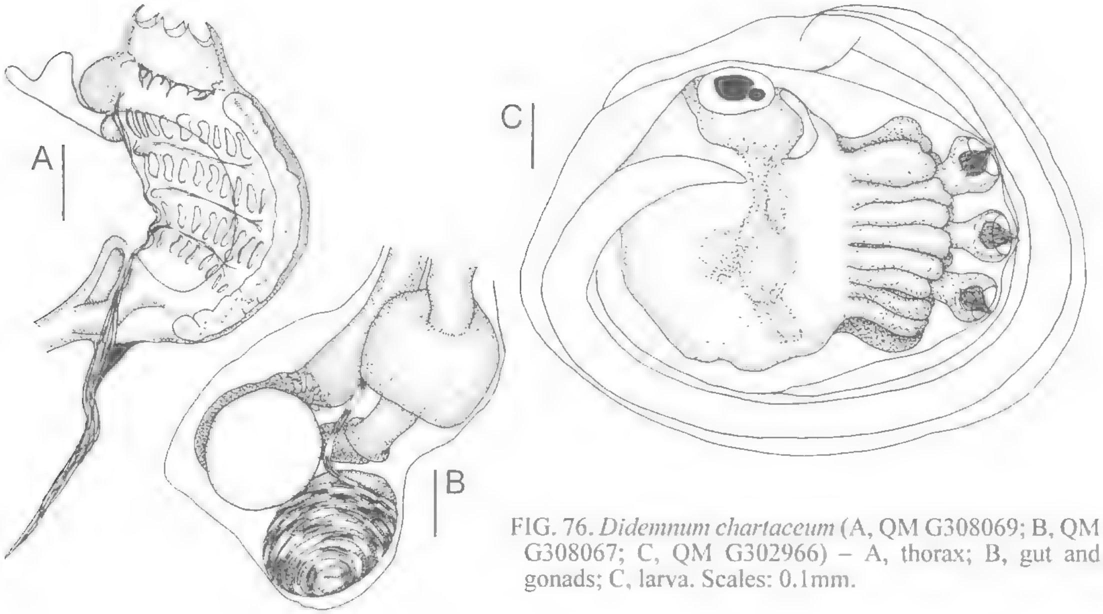


FIG. 76. *Didemnum chartaceum* (A, QM G308069; B, QM G308067; C, QM G302966) – A, thorax; B, gut and gonads; C, larva. Scales: 0.1mm.

label stains brown. The colour of the colony derives from the dark colour of the zooids. The test is translucent.

Spicules are generally to 0.075mm diameter, rarely to 0.09mm. They are of two main types, some stellate with very numerous, short conical pointed rays (to about 30 in optical transverse section), and some almost globular with crowded flat-tipped cylindrical rays.

ZOOIDS. Zooids are small, with the thorax larger than the abdomen. A forked atrial tongue projects from the upper rim of the large atrial aperture which exposes the whole dorsum of the branchial sac directly to the common cloacal cavity. A fine retractor muscle, varying in length according to its state of contraction projects from the postero-ventral corner of the thorax. Nine to 10 stigmata per row are in the branchial sac. The gut forms a rounded almost circular loop, with the proximal part of the ascending limb curved up over the gonads. The duodenum is relatively long and narrow, and the rounded posterior stomach is in the pole of the loop. The rectum is a 'leg of mutton' shape, wide at the proximal end, and has a constriction sharply separating it from the narrow distal end.

The testis is a wide, lens-shaped follicle with 9 coils of the vas deferens around it. Larvae are present in colonies collected from the Swain Reefs (QM G308266) in July, Heron I. (QM G302966) in October, and New Caledonia (Monniot, 1995). They are large and robust, the trunk 0.8mm long, brown, and with about 8 often bifid lateral ampullae along each side of the 3 antero-median adhesive organs. They are brown in the preserved specimens, their colour obscuring their structure. The available larvae are not particularly well advanced, the pharynx of the oozooid not being perforated. Nevertheless, in some newly recorded specimens (QM G302966, G308266), the endostyle of a thoracic bud can be seen in the vicinity of the oesophageal neck (see also Monniot, 1995, fig. 12F).

REMARKS. Spicules are distinctive, as is their distribution in the colony, the crowded bladder cells throughout the test and the dark colour of the preserved material resulting from the dark coloured zooids. However, a variety of colours has been recorded for living colonies, viz. orpiment orange[R] for Fijian material (Kott, 1981), while heliotrope purple[R], magenta[R], as well as brown, and dark and light grey have been recorded for the newly recorded material. Hastings (1931: 98) found that 'the tissues of the Barrier Reef specimen are of a reddish purple colour of such persistence and intensity that unstained preparations have all the appearance of having been stained.' She thought this to have been an artefact of its preservation with other specimens, those and the label, being the same colour. It is more probable that other material in the jar had taken up the colour of this *Didemnum*; and that Hastings was observing the most

conspicuous character of this species — its dark colour in preservative.

The atrial tongue is also an unusual, but not unique, character (occurring also in *D. arancium*, *D. caesium*, and other species). The present species displays a similar range of colours to living specimens of *D. fuscum* and *D. cuculliferum*, although these have white spicules rather than dark pigment in the rims of the cloacal cavities and their spicules differ.

D. multispirale differs in its large, more conspicuously stellate spicules, with fewer and longer conical rays, their bases separated from one another on the central mass. Unlike the present species, the spicules are moderately crowded throughout the colonial test as well as being particularly crowded in the surface. Further, a larval blastozooid has not been detected. When immature, without gonads, *Polysyncraton multiforme*, with similar spicules (although smaller with fewer rays) absent from the middle layer of the colony, could be confused with *D. chartaceum*.

D. nigrum Monniot & Monniot, 1996 is identical with the present species in every known aspect of colony, zooid and larva. Specimens from New Caledonia assigned to *D. obscurum* by Monniot (1995) appear to involve 2 different species neither of which is the Atlantic *D. obscurum* Monniot, 1969. One of the New Caledonian specimens (from the barrier reef) which forms soft lobed colonies with characteristic larvae and spicules (to 0.06mm diameter) appears to be *D. chartaceum*. Larger sheets from the lagoon have spicules to 0.045mm diameter, which are rather small for the present species. *D. chartaceum* is readily distinguished from the Atlantic *D. obscurum* Monniot, 1969. Although larvae are similar, the distinctive spicules of the present species are not present in *D. obscurum*, which has about 13 short, wide but not crowded conical rays in optical transverse section and an 'average' spicule diameter 0.08mm. This suggests a particularly large maximum diameter, larger than the spicules of *D. chartaceum* (including *D. obscurum*: Monniot, 1995 from the barrier reef, New Caledonia) which only rarely reach 0.075mm in diameter. The globular spicules with flat-tipped rays, the marked ventral flexure of the gut loop over the testis, the robust brown larvae and the conspicuous bladder cells that give the test its characteristic consistency are not reported for *D. obscurum*.

Specimens of the present species from the Arabian Gulf (Monniot, C. & Monniot, F., 1997) and probably the Seychelles (Monniot, 1995) extend its known range into the Indian Ocean.

Didemnum clavum sp. nov.
(Figs 77, 172H; Pl. 8C-E)

Didemnum membranaceum Sluiter, 1909: 58 (part, statn37).

TYPE LOCALITY. Queensland (Heron I., filter of aquarium seawater intake, coll. P. Kott 5.3.93, holotype QM G308161; Swain Reefs, Price Cay 20m, coll. S. List 26.7.95, paratype QM G308402).

NEW RECORDS. Western Australia (off Buccaneer Archipelago, QM G300946, G300961, G302914; Legendre I., WAM 515.92; Jurien Bay, WAM 103.93). Queensland (Heron I., QM G308132, G308164, G308171 G308198, G308226, G308337, G308480; Swain Reefs, QM G305681). Northern Territory (Darwin, QM G300930, G302889, G308444).

PREVIOUSLY RECORDED. Indonesia (ZMA TU471.2 Sluiter, 1909).

The species is said to be common in Darwin Harbour on muddy and sandy substrates.

COLONY. Colonies form thin, extensive sheets with a smooth upper surface to more complex colonies with narrow (to 5mm) vertical cylindrical lobes or flattened stalks rising from the surface and sometimes anastomosing with one another (QM G300946, G300961, G302889, G302914, G308444), occasionally forming a rather open basket-work. The living holotype was blotchy pink and white to the naked eye, and other colonies are geranium pink[R], peach blossom[R], flesh colour[R] and white mottled, yellow, orange and madder brown[R]. The orange colony (QM G308132) has a layer of spicules in the surface but few elsewhere. In all other recorded material, the test is crowded with spicules mixed with burnt carmine[R], orange-vermilion[R] or flame scarlet[R] pigment. From Darwin, one colony (QM G308444) was described by the collector as 'red ascidian' and another (QM G300930), said to be purple in life, appears in the in situ photograph to be reddish pink. From the NW coast specimens said to have been respectively black/grey, brown/yellow mottled and black (QM G302914, QM G300961, QM G300946) are all red in the in situ photographs. Zooids are orange-red, orange[R], madder brown[R] or burnt carmine[R] and they show through the surface test with its crowded white spicules. In preservative the colonies are a dirty white colour, the zooids showing through the thin surface test as darker spots owing to the pigment cells retained in the body wall. Some colonies have minute spicule-filled papillae on some parts

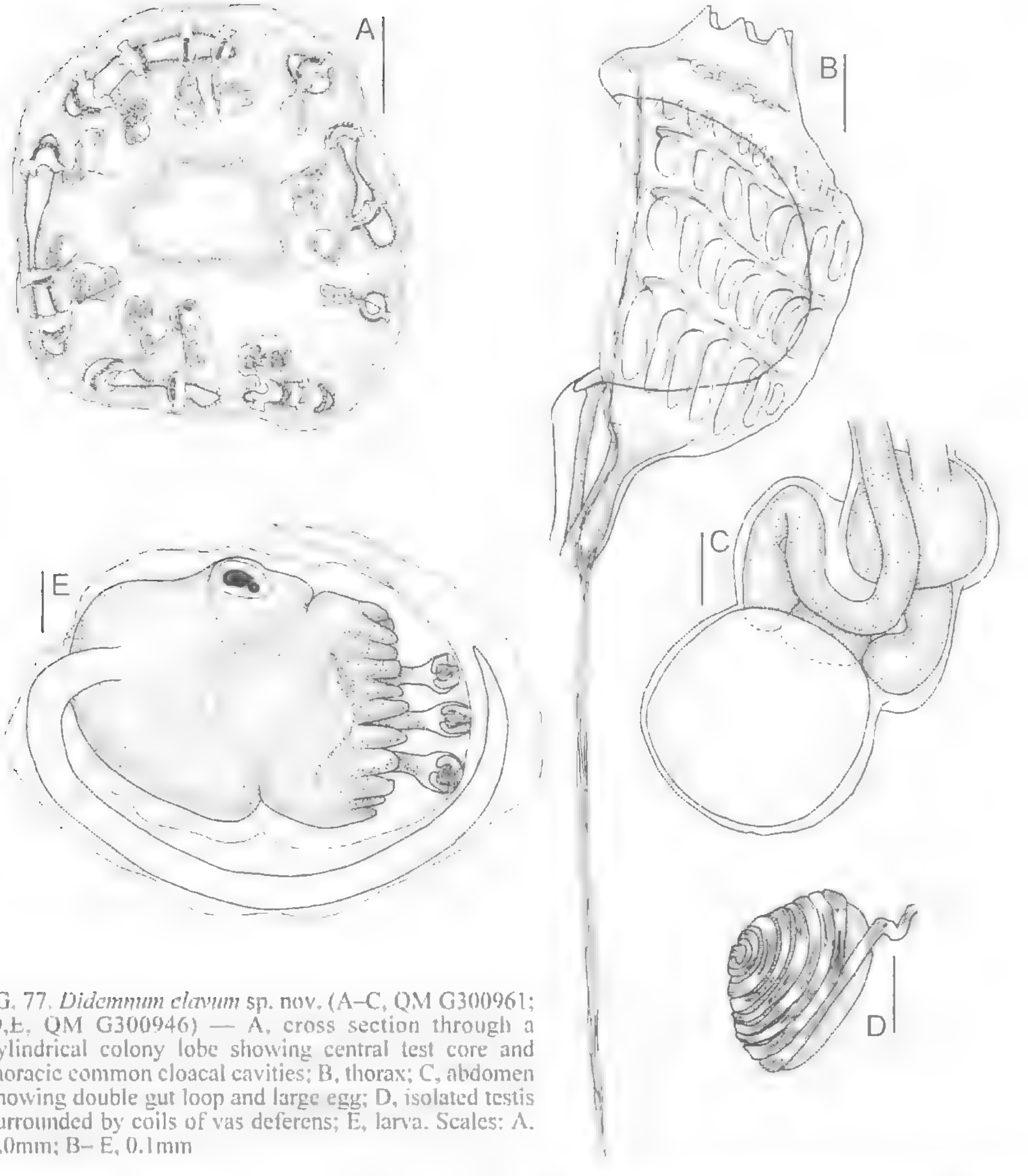


FIG. 77. *Didemnum clavum* sp. nov. (A–C, QM G300961; D,E, QM G300946) — A, cross section through a cylindrical colony lobe showing central test core and thoracic common cloacal cavities; B, thorax; C, abdomen showing double gut loop and large egg; D, isolated testis surrounded by coils of vas deferens; E, larva. Scales: A, 1.0mm; B– E, 0.1mm

or all of the surface and these tend to modify the colour of the colony. The cylindrical vertical stalks in certain colonies have a core of particularly crowded spicules that make a hard axis down through the centre. Sometimes (QM G308171, G308198) a conspicuous hollow papilla is associated with the ventral side of each branchial aperture and one colony (QM G308480) has 6 around each aperture as well as between the apertures. Spicules may outline the margins of the branchial apertures, but are not always conspicuous on the surface. Occasionally (QM G302889) some large vesicles interrupt the spicules in the surface test.

The common cloacal cavity is thoracic, occasionally quite shallow, but deeper in the upright lobes of a more complex colony from Darwin (QM G308444). Thoraces cross the cavity in independent test sheaths. Abdomina are embedded in the basal test, but occasionally (QM G308198) the common cloacal cavity extends

almost the whole length of a group of zooids, leaving the abdomina clumped together and projecting up into the common cloacal cavity. Common cloacal apertures are large, sessile, their margins frilled, and they occur randomly, but generally on elevated parts of the surface. Cylindrical colony lobes with a rod of central test strengthened with particularly crowded spicules, have the abdomen embedded around the outside of this axial test core.

Spicules are generally 0.03–0.06mm in diameter but occasional giant spicules with 4–6 long, narrow spiky rays up to 0.1mm occur. Most spicules have particularly long, narrow rod-like rays with pointed or occasionally blunt tips. There generally are only 5–7 rays in optical section and rarely 9. Ray length/spicule diameter is in the vicinity of 0.4. Only relatively few spicules with shorter conical rays occur.

ZOOIDS. Zooids are about 1mm long. The branchial siphon is short with 6 conspicuously pointed lobes around the aperture. The thorax is robust, with 9 stigmata in the anterior row, 8 in the next 2 rows and 7 in the last row. A long, tapering retractor muscle projects from the long, narrow oesophageal neck one third, to halfway down it. The ascending limb of the long gut loop is kinked up over the testis. Gonads are mature in ZMA TU471.2 (formerly a syntype of *D. membranaceum*) from Indonesia as well as in newly recorded colonies from Heron I. (QM G308171), and NW Australia (QM G300946, G300961, G302914). The testis is hemispherical, and the vas deferens spirals 8 times around its outer, domed surface, sometimes almost completely covering it — leaving only a small area toward the base exposed but with the proximal spiral wide, exposing a considerable area at the apex of the testis. Larvae are present only in specimens from NW Australia collected in August (QM G300946, G300961). They are robust, oval, the trunk 0.7mm long without a pronounced waist. Eight thick ectodermal ampullae are along each side of the 3 antero-median adhesive organs and the tail winds two-thirds of the way around the trunk. The adult organs are not well advanced, stigmata are not perforated and it is not known whether or not blastozooids develop as they usually do in other species with numerous ectodermal ampullae and a thick trunk without a waist.

REMARKS. Except for the variable occurrence of surface papillae, variations in depth of the thoracic cloacal cavity and development of upright lobes on the surface, characters of the known specimens are remarkably consistent, viz. similar gonads and branchial sacs, inconspicuous branchial apertures, unique long rod-like spicule rays and occasional giant spicules with relatively few spiky rays. Spicules differ from those of *D. membranaceum* and *D. cuculliferum* by their greater diameter, and their longer, straighter and fewer rays. The giant spicules resemble those of *D. membranaceum* and *D. cuculliferum* but occur less frequently. The vas deferens coils 8 times (as in *D. cuculliferum*, but only 6 times in *D. membranaceum);* and the branchial sac of the present species has relatively numerous stigmata.

The echinated surface with minute spicule-filled papillae occur in many *Didemnum* spp. Also, similar pointed spines are often associated with each branchial aperture in *D. cuculliferum*, *D. membranaceum*, *D. scopi* and *D. stragulum* while the surface of the spiky colony (QM G308480) resembles *Polysyncraton echinatum*.

Didemnum complexum sp. nov.
(Figs 78, 170E)

Didemnum lambitum: Kott, 1972c: 249 (part, specimen without larvae).

TYPE LOCALITY. New South Wales (Port Hacking, Little Turiel Point, 60-70m on rock walls and clumps and ceilings of caves, coll. C. Lawler and URG 20.5.69, holotype AM Y820).

FURTHER RECORDS. New South Wales (North Head Sydney Harbour, QM G303748). Tasmania (Triabunna, SAM E2859).

COLONY. Colonies are large (to 10cm or more in greatest dimension), often complex, and usually brittle and broken into several pieces. The holotype is an encrusting base with the surface extended into crowded lobes and long branches, each with a terminal common cloacal aperture. Other colonies consist of thin sheets, over conglomerates of rubble, pebbles, shell and worn fragments, from the surface of which vertical plates and finger-like lobes protrude, anastomose with one another and create a complex fenestrated 3-dimensional mass. The basal sheet of all colonies has basal and surface layers of test separated by thoracic common cloacal cavities, the upright lobes and lamellae sometimes have a central test core, separated from the zooid-bearing layer by common cloacal spaces crossed by test connectives. Zooids open all around the outer surface of the protuberances. The surface is raspy to the touch, and in one colony (QM G303748) is covered with minute papillae between the slightly protuberant stellate

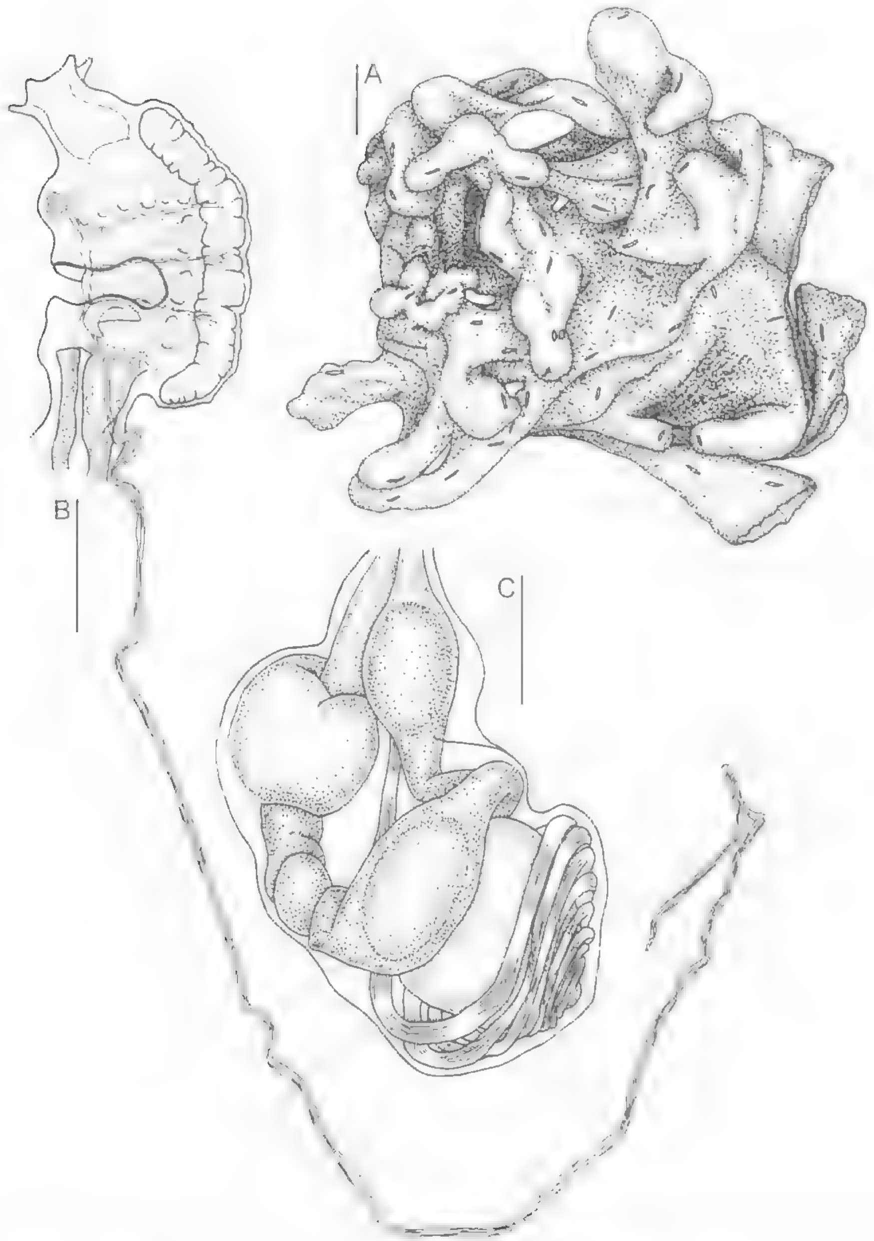


FIG. 78. *Didemnum complexum* sp. nov.(A, QM G303748; B,C, AM Y820) – A, colony showing common cloacal apertures, B. thorax showing long retractor muscle (folded up); C, abdomen with bent up gut loop and coiled vas deferens around undivided male follicle. Scales: A, 1.0mm; B,C, 0.1mm.

branchial apertures. The rims of the apertures are outlined in spicules, which project in to line the siphons. Spicules are present throughout the test. They are generally to 0.06mm in diameter with 7–9 moderately long and sharply pointed conical rays in optical transverse section. Ray length/spicule diameter is about 0.4. Spicules with round-tipped rays were not detected, rays being uniformly conical and pointed. Occasional giant spicules about 0.075mm diameter with a total of 4–6 broad-based conical rays were detected. Sometimes these giant spicules are a 2-dimensional cross.

Zooids are in clumps, surrounded by deep primary cloacal canals with the surface test depressed over them. Thoraces are partially embedded in solid test or cross the thoracic cloacal cavity in separate test sheaths. Abdomina usually are embedded in the test connectives joining the surface to the central test core or basal test across the cloacal cavity. The living holotype specimen was described as 'candlegrease' ascidian and was fleshy pink and pale yellow.

ZOOIDS. Zooids are small with short branchial siphons and a large sessile atrial aperture exposing the branchial sac directly to the cloacal cavity. A long fine retractor projects from the top of the oesophageal neck. Only about 6 stigmata are in the anterior row of the branchial sac. Eight coils of the vas deferens surround the lens-shaped testis.

REMARKS. The spicules are similar to those of *D. membranaceum*, although the giant spicules of the latter species have long narrow, spiky arms. Both species have small zooids. However, *D membraenaceum* never has lobed 3-dimensional colonies with extensive common cloacal cavities, its zooids are slightly larger, the thoraces more comma shaped and it has 6 (rather than 8) coils of the vas deferens.

D. spongioide and *D. roberti* have complex 3-dimensional colonies like the present one, although their colony lobes are of greater diameter and their cloacal cavities more extensive than the present species. *D. roberti* is further distinguished by the distribution of spicules confined to a layer in the surface and another in the base of the colony, and its tough, gelatinous colony, (rather than hard, brittle ones of *D. spongioide* and the present species). Spicules of *D. roberti* and *D. spongioide* also are similar to the present species although in the former the rays are longer and in the latter are shorter.

Larvae referred to by Kott (1972c) are not in the holotype of the present species but in a specimen of *D. lissoclinum,* which Kott (1972c) also had assigned to *D. lambitum.*

Didemnum crescente sp. nov.
(Figs 79, 172F)

Didemnum augusti: Kott, 1976: 68.

TYPE LOCALITY. New South Wales (Eden, coll. A.R. Davis TBA5 December 1996, holotype QM G308495).

FURTHER RECORDS. Tasmania (Triabunna, SAM E2854). Victoria (Western Port – MV F68801 Kott, 1976; Mallacoota Inlet – Kott, 1976)

COLONY. The holotype is a small thin sheet but the other known colonies are more extensive. Clumps of 6 or 7 zooids are in circular to longish oval area surrounded by surface depressions over deeper common cloacal canals lined on each side by zooids. These canals sometimes extend into vast posterior abdominal spaces interupted only occasionally by connectives that attach the upper zooid layer of the colony to the basal test. Shallow canals penetrate the clumps of zooids at thoracic level. The basal layer of test (beneath the zooids) is one-third of the total thickness of the colony and the thoracic and abdominal levels are a third each.

Spicules are evenly spaced throughout the test, and are especially crowded in the lateral organs, which frame the posterior end of each side of the thorax in a conspicuous crescent of crowded spicules. Spicules are to 0.07mm in diameter and have 7–9 relatively long, sturdy, conical rays in optical transverse section with a ray length/ spicule diameter ratio to 0.375. The stellate branchial apertures are lined with spicules.

The colony is white in preservative.

ZOOIDS. Zooids are small. The branchial siphon is short with 6 relatively shallow lobes. The atrial aperture is large and sessile without an anterior tongue. The lateral organ is a large flap of the parietal body wall that lies over the crescentic mass of spicules along the edge of the test sheath at the posterior end of the thorax. A long, fine retractor muscle projects from halfway down the long oesophageal neck. The branchial sac has 7 stigmata in the anterior row. The gut forms a relatively short, rounded loop. In the holotype and the large Tasmanian specimen 9 coils of the vas deferens surround an undivided, markedly conical testis. However, neither mature gonads nor embryos are in the large colony from Western Port.

Embryos are being incubated in the basal test of the holotype. The larval trunk is 0.6mm long, and 4 club-shaped ectodermal ampullae are along each side of the 3 median adhesive organs. The tail is wound two-thirds of the way around the trunk. A horizontal lateral ampulla is on the left.

REMARKS. The species resembles *D. patulum* in some respects but the spicules have longer and fewer rays. *D. incanum*, the common species off the New South Wales coast, has smaller spicules than those of the present species and its cloacal systems are different, although otherwise the species are similar. The large horizontal posterior abdominal cloacal cavity, sturdy stellate spicules

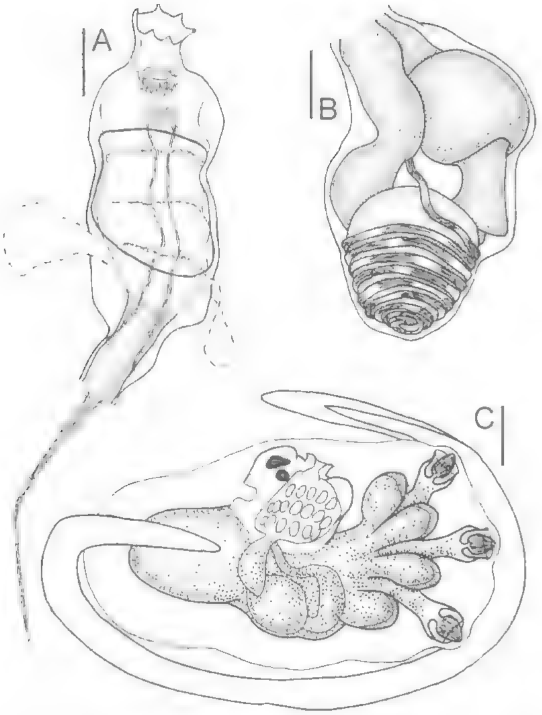


FIG. 79. *Didemnum crescente* sp. nov. (QM G308495) – A, thorax with lateral organs projecting from the parietal body wall; B, abdomen with gut loop and testis with coiled vas deferens; C, larva. Scales: 0.1mm.

and crescent-shaped flap-like external lateral organs are distinctive in all examined specimens.

Didemnum cuculliferum (Sluiter, 1909) (Figs 80, 173C; Pl. 8F)

Diplosomoides cuculliferum Sluiter, 1909: 90.
Didemnum cuculliferum: Kott, 1981: 164.
Not *Didemnum cuculliferum*: Monniot, 1995: 305 (part< *D. stragulum*).
Didemnum turritum Michaelsen, 1930: 521.
Not *Didemnum turritum*: Kott, 1962: 319 (<*D. lissoclinum*); 1976: 66 (<?*Polysyncraton* sp.).
Didemnum nekozita Tokioka, 1967: 67.
Didemnum anoi Monniot & Monniot, 1987: 25.
Didemnum moseleyi: Eldredge, 1967: 210 (part, from Eniwetak).

NEW RECORDS. Queensland (Capricorn Group, QM G308030, G308190, G308242-4, G308259; Lizard I., AM Z5120-1).

PREVIOUSLY RECORDED. Western Australia (Shark Bay – ZMH K1701syntypes *D. turritum* Michaelsen, 1930); Indonesia (ZMA TU490 holotype *D. cuculliferum* Sluiter, 1909). Palau Is (Tokioka, 1967; Kott, 1981). Eniwetak (Eldredge, 1967). Philippines (Tokioka, 1967). Fiji (QM G12594 Kott, 1981). French Polynesia (Monniot & Monniot, 1987).

COLONY. The newly recorded colonies are small oval cushions about 1cm or less in maximum extent, 3mm thick with rounded borders. The star-shaped branchial apertures scattered over the surface are outlined by spicules that project down into the siphonal lining, and sometimes appear to entirely fill the 6 lobes of the stellate aperture. With few exceptions (see QM G308190), a conspicuous hollow pointed papilla projects out from the ventral side of each branchial opening on some or all parts of the colony surface (see also Sluiter, 1909; Tokioka, 1967); and on some colonies (e.g. QM G308190) minute spicule-filled papillae are also on the surface between the zooid openings. A thin superficial layer of bladder cells overlies the spicules which otherwise fill the very thin surface test, interrupt the bladder cells over the anterior end of each zooid and extend up into the papillae that project from the surface. The large pointed ventral papilla usually present on each branchial aperture accommodates the ventral branchial lobe of the zooid. This spine is pulled down over the aperture when it is contracted and the zooid is pulled down into the colony.

The surface test has a collapsed (loose) appearance in the preserved material. This possibly is because it is particularly thin. Pressure in the large cloacal cavity (that occupies the whole length of the thorax and extends to abdominal level around clumps of zooids) usually would inflate the living colony and keep it turgid. Spicules are crowded throughout the test, but the colonies are soft, owing to the large cloacal cavity and thin layer of surface test. Abdomina occasionally are embedded in basal test but when that is thinner, clumps of abdomina rise above the basal test, and project up into the cloacal cavity. At thoracic level, the cloacal cavity penetrates around each thorax with its ventral sheath of test, and the large atrial aperture exposes much of the branchial sac directly to the cloacal cavity.

Most spicules have relatively few (5–7) rod-like cylindrical rays (with blunt tips) in optical transverse section and generally are not more than 0.04mm in diameter. Giant spicules up to 0.075mm in diameter with 4–6 long spiky rays are scattered sparsely amongst the smaller spicules. The ray-length/spicule diameter ratio is 0.4.

In the newly recorded living colonies the pigment in the superficial layer of test is poppy[R], coral red[R], or dragons blood red[R]. Pigment cells are in the superficial test of living colonies, mixed

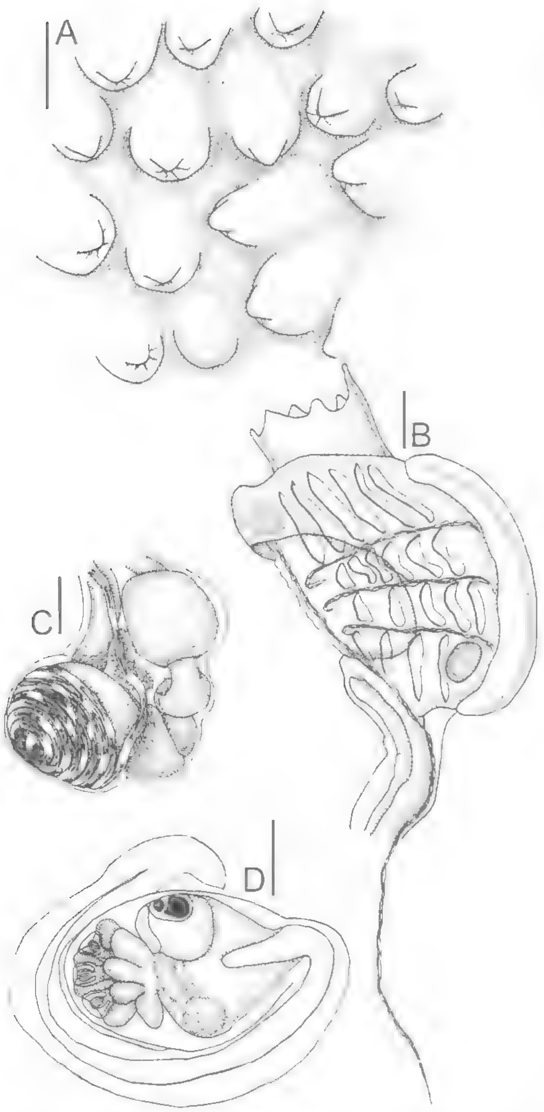


FIG. 80. *Didemnum cuculliferum* (A,B, QM G308243; C, QM G308259; D, QM G308190) – A, external surface showing enlarged ventral papilla associated with each branchial aperture; B, thorax with ventral branchial lobe enlarged; C, abdomen showing testis and coiled vas deferens; D, larva. Scales: A, 0.5mm; B–D, 0.1mm.

with the bladder cells. Zooids are scarlet[R] or scarlet vermilion[R]. *Prochloron* sometimes is present on the surface and the common cloacal apertures, more or less in a row down the centre of the colony, have greenish-yellow rims owing to the green plant cells overlying the white spicules. Pigment is missing around the branchial apertures which are white, owing to the white spicules. The colonies are white in preservative, and zooids are yellowish with greenish yellow stomach and proximal part of the rectum.

ZOOIDS. Zooids are about 1mm long. The branchial siphon is a short wide cylinder with 6 conspicuous pointed lobes. The ventral branchial lobe is enlarged to fit into the pointed test papilla on the surface when one is present. Six stigmata are in each of the 2 anterior rows, 5 are in the last 2 rows. A small lateral organ is toward the posterior end of the thorax near the edge of the atrial aperture. A long, narrow retractor muscle is free from the middle part of the relatively long oesophageal neck. The gut loop is moderately long, and its posterior pyloric part is bent at a right angle to the proximal part. A V-shaped mass of what appears to be glandular material is in the gut loop. Two club-shaped vascular appendages project out into the test from the ventral (concave) side of the gut loop.

A large egg and/or dome-shaped male follicle, the latter with the vas deferens coiled around its outer surface 8 times, are against the dorsal side of the distal end of the gut loop where it is bent up against the anterior part of the loop.

Larvae from the Palau Is (Tokioka, 1967) are reported to have a trunk 0.7mm long, and to be like the larvae of *D. moseleyi* (with 4 pairs of lateral ampullae and the usual otolith and ocellus). Monniot & Monniot (1987) recorded a trunk length of 0.6mm for a larva of *D. cuculliferum*. The larva of *D. anoi* Monniot & Monniot, 1987 has a trunk 0.43mm long. Larvae from Heron I. (QM G308190), collected in March, have a larval trunk 0.3–0.4mm with the tail wound about three quarters of the distance around it. All recorded larvae have 4 pairs of lateral ampullae.

REMARKS. The thin surface test and extensive cloacal cavity, together with the small spicules with their relatively few cylindrical rays, and occasional giant 4–6-rayed spicules scattered amongst them distinguish this species. The hollow pointed surface papilla associated with each branchial aperture is a useful character when present, but occasionally it does not occur. Always the V of glandular(?) material is in the gut loop and origin of the retractor muscle is from halfway down the oesophageal neck. However, these characters occur in other species. Tokioka (1967) misinterpreted the vascular appendages from the ventral side of the gut loop as large club-shaped 'circum-intestinal glands'. The testis follicle tapering to a pointed cone as

reported in the Fijian material Kott (1981) occurs in *D. sphaericum* Tokioka, 1967 and in some newly recorded specimens of *D. candidum*, but is not present in the newly recorded specimens of the present species.

Colonies with a characteristic pointed papilla associated with each branchial aperture (as in the holotype of *D. cuculliferum* ZMA TU490) are reported for *D. nekozita* Tokioka, 1967, *D. cuculliferum*: Kott, 1981 and *D. cuculliferum*: Monniot & Monniot, 1987 and all these appear to be conspecific. Tokioka (1967) reported giant spicules for his Palau Is specimens; and although Kott (1981, fig. 16d) showed spicules only up to 0.06mm she referred to large spicules both in the Fijian material and in the type. Re-examination of this material has confirmed that the characteristic giant spicules with few, long spiky rays are present. In view of the agreement in other aspects of the colony and zooids it is probable that these giant spicules were overlooked also in the French Polynesian material (Monniot & Monniot, 1987). *D. turritum* Michaelsen, 1930 from Shark Bay (WA) has colonies characteristic of the present species with extensive common cloacal cavities, and spicules with similar numbers of rays and in the same size range. *D. anoi* Monniot & Monniot, 1987 also has similar colonies, spicules and larvae. The reversed gut loop referred to by Monniot & Monniot (1987) for *D. anoi* is not understood. The gonads are in the same position in relation to the ascending and descending limbs of the gut loop and the appearance of reversal may be the result of distortion of some of the zooids. This view is supported by the unusual position of the retractor muscle shown (Monniot & Monniot, 1987, fig. 6D). The specimen of *D. moseleyi*: Eldredge, 1967 from Eniwetak with its rod-shaped spicule rays and occasional giant spicules probably belongs to the present species, which is readily and more reliably identified by these spicules than by the hollow papillae.

D. cuculliferum: Monniot, 1995 from New Caledonia has pointed papillae associated with the ventral lobe of each branchial aperture. However, its large stellate spicules (to 0.08mm diameter) with conical rays are not a feature of the present species. They resemble the spicules of *D. stragulum* which has similiar spicule-filled papillae on the surface although usually the colonies are larger. However, since the vas deferens coils recorded by Monniot (1995) vary between 5 and 9, it is probable that more than one species is involved in this record.

D. sphaericum and *D. candidum* have spicules with cylindrical rays, similar to those of *D. cuculliferum* although neither of the first 2 species has giant tetrahedral or 6-rayed spicules. *D. fuscum* which Tokioka (1967) believed to have spicules similar to the present one, has more numerous rays, generally larger spicules and lacks the giant ones.

D. membranaceum and *D. clavum* also have giant tetrahedral or 6-rayed spicules but the majority of their spicules are larger with longer rays than the present species. Also, *D. membranaceum* spicules have more numerous and more pointed rays. The present species has (like *D. clavum)* more coils of the vas deferens than *D. membranaceum* although it has the same number of stigmata.

D. turritum: Kott, 1962 (from South Australia AM Y1528-31) has similar (but inconspicious) surface papillae associated with each aperture, and similar cloacal systems to *D. cuculliferum*, but it has larger spicules and fewer vas deferens coils than the present species and it lacks giant spicules. It appears to be conspecific with *D. lissoclinum*.

Similar pointed papillae are present on the surface of *Polysyncraton echinatum*, *Didemnum clavum*, *D. cygnuus*, *D. membranaceum*, *D. scopi*, *D. stragulum* and *D. turritum*: Kott, 1976 from Western Port (?*Polysyncraton* sp.).

D. cuculliferum occurs over a wide geographical range. The large intraspecific range in larval size (trunk length 0.3–0.75mm) is unusual.

Didemnum cygnuus sp. nov.
(Figs 81, 170H)

TYPE LOCALITY. Western Australia (Rocky Bay, Swan River estuary on seagrass, coll. Vas Hosja 3.6.92, holotype WAM 362.92).

FURTHER RECORDS. Western Australia (off Port Hedland, WAM 6.93 130.93).

COLONY. All recorded specimens are tough and irregular, but thin, sheets growing over rocks, sea-grass or debris. In preservative, colonies are cream with conspicuous evenly spaced stellate branchial apertures. The holotype has a small pointed papilla on the ventral side of each branchial aperture, drawn down over the aperture when the zooid contracts. Spicules are crowded in the surface test, continue down into the siphonal linings and fill the pointed papillae. They form a distinct layer in the surface, around the common cloacal cavity and on the base of the colony, but are relatively sparse elsewhere.

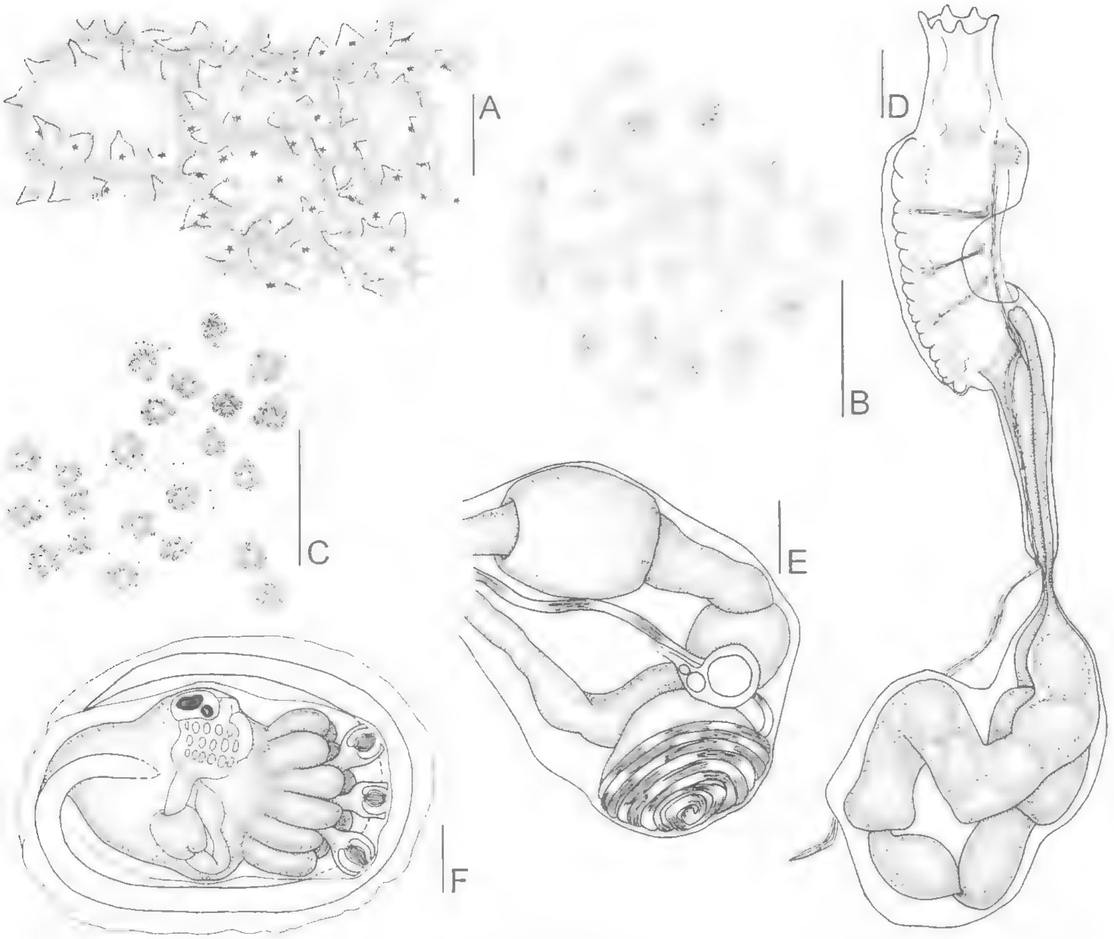


FIG. 81. *Didemnum cygnuus* sp. nov. (A,E, WAM 362.92; B,D, WAM 6.93; C,F, WAM 130.93) – part of colony surfaces. A, showing pointed papillae on ventral side of each branchial aperture; B, showing branchial apertures without surface papillae; C, showing spicules in petal-like clumps around each branchial aperture; D, whole zooid; E, abdomen with gonads; F, larva. Scales: A–C, 1.0mm; D–F, 0.1mm.

Both specimens from Port Hedland have smooth surfaces and lack the pointed papillae which, in the holotype, are associated with each branchial aperture. Some spicules line the common cloacal spaces around the zooid. In one specimen (WAM 130.93) they are concentrated into daisy like patterns around each branchial aperture (rather than being in an even layer) and are scattered sparsely in the basal test. In the other specimen (WAM 6.93) the thin surface layer of test has a single layer of evenly but sparsely distributed spicules, crowded in a plug in the lining of each branchial siphon, or sometimes outlining the stellate apertures. Spicules are also sparse in the test around the zooids, and are missing from the basal test.

Zooids are arranged along each side of the deep branching common cloacal canals, which converge to randomly distributed openings. The primary common cloacal canals extend vertically through almost the whole depth of the colonies and continue into posterior abdominal spaces. In the holotype these primary common cloacal canals are more or less visible from the surface as grey lines with branchial apertures along each side. They surround zooid-free stands of test, although sometimes zooids and some thoracic or oesophageal canals penetrate into these areas. Sometimes solid stands of test between the

common cloacal canals cause slightly elevated ridges of test on the surface of the colony. The zooids are embedded in these stands of test, leaving their branchial sacs directly exposed to the cloacal canals through the open atrial apertures. A high ridge of spicule free test also surrounds the margin of the colony.

Spicules are stellate but asymmetrical. Often they are so spread out and distant from one another that, even to the naked eye, differences in their sizes are particularly conspicuous, as is their stellate shape with relatively few rays. Sometimes they appear like tiny stars in the surface of the colony. Nevertheless, maximum distance between tips of the rays on any spicule is no more than 0.07mm. Generally 5–7 and occasionally 9 rays are in optical transverse section. Sometimes one of the rays is larger than the others, or rays are developed only on one side, and one spicule with a ring of about 10 rays around an axis, rather like a cock's comb, was observed (WAM 6.93). The rays are often broadly based conical ones, but sometimes they are flattened or angular in section.

ZOOIDS. Zooids are relatively long (1.5mm). Branchial apertures with 6 pointed lobes are on a distinct cylindrical siphon about half the length of the thorax. The oesophageal neck is about the same length as the thorax. The post-pyloric part of the gut loop is bent up to form a secondary loop. Zooids could not be removed from the test. Round-tipped columnar cells project from the body wall. A long tapering retractor muscle is free from about halfway down the oesophageal neck. About 8 stigmata are in each row, but these could not be counted accurately. The testis has 8 coils of the deferens around it.

A few tailed larvae are in the basal layer of test of colonies collected in October and June respectively (WAM 130.93, 362.92). Unfortunately they are not at an advanced stage of development. The tail is wound only halfway around the trunk, which is 0.5mm long. Four epidermal ampullae are along each side of the antero-median adhesive organs. An otolith and ocellus are present, but stigmata were not detected.

REMARKS. The arrangement of the zooids along each side of the deep cloacal canals together with the single, sometimes sparse layer of spicules in the surface test is distinctive as is the irregular form of the rather robust looking spicules with relatively few broadly-based conical but sometimes flattened or triangular rays. The spicules are occasionally reminiscent of some asteroid echinoderms (e.g. *Asterina* sp.). The 3 known colonies of this species have quite different concentrations of spicules in the surface. However, the similarity of the spicules and of the colony form together with the location of the spicule layers suggest they are conspecific.

D. guttatum Monniot & Monniot, 1996 has long branchial siphons and similar but larger spicules, with a few more rays (7–9 in optical transverse section). *Didemnum* species with stellate spicules confined to limited layers of the test, viz. *D. caesium*, *D. roberti*, *D. fragum*, *D. linatum*, *D. pecten*, have more regularly stellate spicules with more rays. The papillae associated with the apertures in the holotype are like those found in *D. cuculliferum* and other species (see *D. cuculliferum* Remarks).

The type locality, just inside the Swan River Estuary, although not subject to strong tidal influences, would certainly be exposed to lowered salinity, especially during winter when the present specimen was collected.

Didemnum delectum sp. nov.
(Figs 82, 171H; Pl. 8G)

Didemnum moseleyi: Kott, 1972a: 19 (part, specimen from West I.); 1972b: 179 (part, specimens from Investigator Strait and Elliston Bay).

TYPE LOCALITY. South Australia (SW of Ceduna, Tourville Bay, Bonaparte Creek on bryozoan clump 6–8m, coll. W. Zeidler, K. Gowlett Holmes, B.J. McHenry 5.3.93, holotype SAM E2632; West I. boulder slope, coll. S.A. Shepherd 27.5.71, paratype SAM E2662; Investigator Strait, depth 31m, coll. J. Watson 17.1.71, paratype SAM 2661).

FURTHER RECORDS. South Australia (Elliston Bay – SAM E2830 Kott, 1972b; Yorke Peninsula, SAM E2625 E2627; Tipara Reef, SAM E2674; Upper Spencer Gulf, SAM E2840, E2844; St Vincent Gulf, SAM E2831; West I. – SAM E2699 Kott, 1972a).

COLONY. Colonies are soft and flexible in preservative. Spicules are present throughout. Branchial apertures are conspicuously stellate with spicules outlining them, and occasionally they are slightly depressed into the surface. Sometimes some small rounded spicule-filled papillae are crowded on the surface of the colony. Terminal common cloacal apertures are sessile and open on the rounded domes, lobes and lamellae that have basal test projecting up into their centres and zooids opening all around their outer surfaces. The preserved colonies sometimes look spotted owing to the thin surface test through which the darker zooids can be seen. In life, one colony (SAM E2699) is said to have

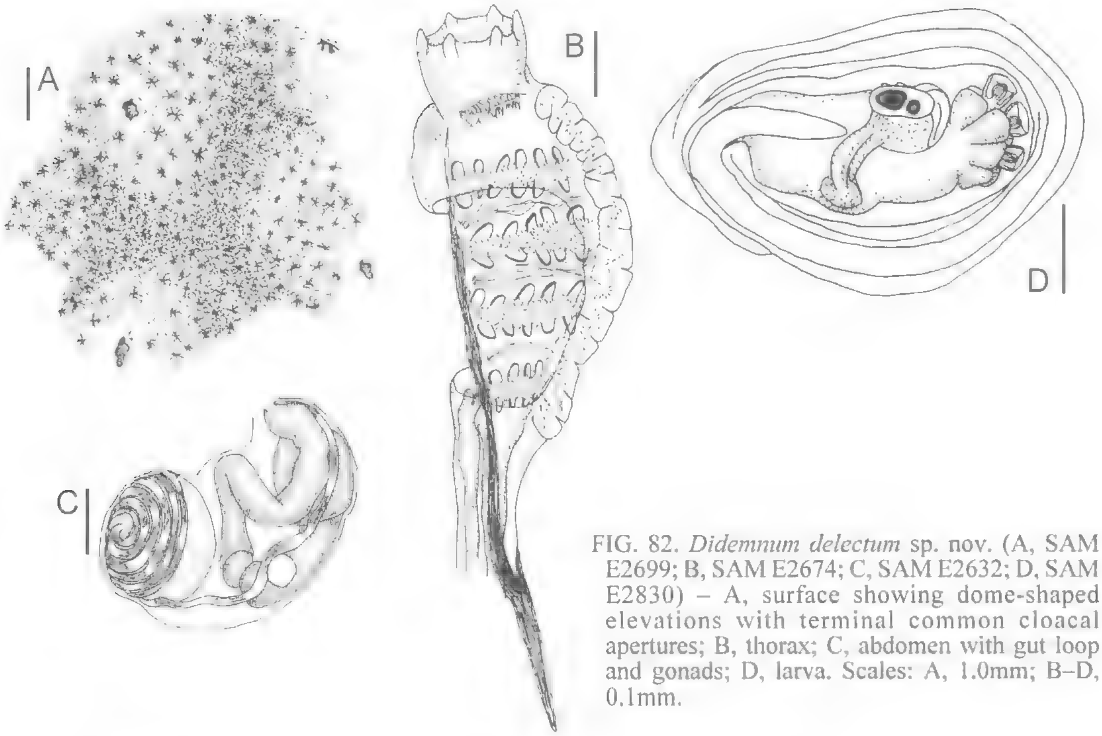


FIG. 82. *Didemnum delectum* sp. nov. (A, SAM E2699; B, SAM E2674; C, SAM E2632; D, SAM E2830) – A, surface showing dome-shaped elevations with terminal common cloacal apertures; B, thorax; C, abdomen with gut loop and gonads; D, larva. Scales: A, 1.0mm; B–D, 0.1mm.

been cream coloured but photographs show most colonies to be pale pink.

The surface layer of test (over the cloacal cavity) is thin and contains a thin superficial layer of bladder cells and a single layer of crowded spicules. The thoracic cloacal cavity is relatively deep and thoraces cross it each in a separate ventral test sheath. The abdomina are embedded in the basal test, but the zooids sometimes are so crowded that there is very little test between them. Also, although the common cloacal cavity usually extends the whole length of the thoraces, sometimes it is even deeper and extends the full depth of the zooids or posterior to them, clumps of abdomina being suspended in columns of test attached to the floor of the common cloacal cavity. Flexibility of the colonies is enhanced by large common cloacal cavities, thin surface test, and the small amount of test between crowded zooids.

Spicules are up to 0.04mm diameter but most are smaller, being 0.02–0.035mm. They have 7–9 long, narrow conical and pointed rays in optical transverse section. The ray length/spicule diameter ratio sometimes exceeds 0.4.

ZOOIDS. Zooids, about 1mm long, have short but robust, and sometimes tulip-shaped, branchial siphons with 6 points around their rims. Only 6 oval stigmata are in the anterior row in the branchial sac, and 4 are in the posterior row, which has shorter stigmata. The posterior row sometimes is obscured completely when the zooid is contracted. The atrial aperture is a large, sessile opening, without an atrial lip. A large lateral organ is about two-thirds of the way down the edge of the atrial aperture. A long, fine, tapering, retractor muscle projects out into the test from at least halfway down the oesophageal neck. The post-pyloric part of the gut loop is flexed ventrally. Testes in the holotype and in specimens collected in April and May (SAM E2625, E2830) are undivided, and surrounded with 6 coils of the vas deferens.

Small larvae are in the basal test of a specimen from Elliston Bay collected in May (SAM E2830). The trunk (0.35mm long) has the tail wound the whole way around it. A large ocellus and otolith are in the middle of the upper surface, 4 lateral ampullae are on each side of the 3 antero-median adhesive organs and a large horizontal ampulla projects backwards on the left side of the trunk from behind the adhesive array.

REMARKS. Small zooids, small stellate spicules with regularly conical rays, a thin layer of surface test over the large thoracic common cloacal cavity and thickened basal test beneath the

common cloacal apertures characterise this species. *D. membranaceum* has larger spicules with similar but longer pointed rays and characteristic giant spicules.

Size and form of the spicules distinguish this species from most other sympatric South Australian species. *D. microthoracicum* also has a small thorax, but although its spicules are of similar form, they are larger. *D. macrosiphonium* has smaller spicules with shorter, and more numerous rays and a long branchial siphon. Colonies of *P. orbiculum* Kott, 1962 are similar to the present species but have larger spicules with more rays and characteristic vesicles in the surface test.

D. incanum (Herdman, 1899) from NSW, has many characters in common with the present species, although its colonies are less robust, its thoraces narrower with slightly fewer stigmata, 9 (rather than 6) coils of the vas deferens and smaller spicules with relatively short, broad rays.

Didemnum effusium sp. nov. (Fig. 83A,B)

TYPE LOCALITY. South Australia (Kingston, sheltered location near jetty, coll. J.E. Watson September 1977, syntypes QM G10139).

FURTHER RECORDS. Victoria (Hobson's Bay, MV F68759).

COLONY. The syntype colonies are small, irregular, often long (to about 2cm), narrow and slightly branching cushions. Zooids can be seen through the firm, gelatinous, milky and slightly translucent test. The capacious cloacal cavity is thoracic. However, the large colony from Victoria is an upright flattened plate partially divided into vertical lobes which fuse with one another along their length. They have a fleshy central core which is partially separated from the outer zooid-bearing layer by posterior abdominal cloacal spaces. Cloacal spaces also penetrate amongst the zooids at thorax level. All the colonies are completely aspicular.

ZOOIDS. Zooids are relatively large, to about 1.5mm long, even when the thorax is very contracted. The branchial siphon is long and cylindrical and the aperture has 6 short pointed lobes around the rim. The atrial aperture is wide open, exposing most of the branchial sac directly to the cloacal cavity. There is no atrial lip. Four rows of stigmata were detected but the thoraces are too contracted for the number in each row to be determined. In some zooids, large, spoon-shaped lateral organs project from each side near the posterior end of the thorax with the concavity directed ventrally. The retractor muscle is long and tapering, separating from the oesophageal neck about halfway down. The abdomen is robust. The diameter of the post-pyloric part of the gut is relatively thick and that part of the loop is flexed ventrally. The testis is undivided and lies on the dorsal side of the flexed part of the gut loop. It is surrounded by 10 vas deferens coils.

Larvae are present in the Victorian specimen (collected in April). The trunk is 0.4mm long, the tail is wound about halfway around it and 4 finger-like ectodermal ampullae are along each side of the 3 antero-median adhesive organs.

REMARKS. The only other completely aspicular didemnids (apart from *Diplosoma* spp.) known from South Australian waters are *Trididemnum pseudodiplosoma* (Kott, 1962), and *T. nobile*. In addition to the generic differences, including their posteriorly oriented atrial siphons and large 3 dimensional common cloacal cavities, *T. nobile* has very complex colonies and larger zooids than the present one; and *T. pseudodiplosoma* has its test packed with bladder cells, small zooids, a short retractor muscle from the top of the oesophagus and a larva with an abundance of blastozooids. *Didemnum minisculum* is a temperate species that forms small, soft, translucent colonies, but it does have spicules, its retractor muscle projects from the top of the oesophagus and it has only 6 coils of the vas deferens. The tropical *D. jedanense* sometimes has aspicular colonies, but it has only 7 coils of the vas deferens.

Although the syntypes are smaller colonies than the Victorian specimen, the zooids with their long branchial siphon, and numerous coils of the vas deferens, are identical.

The large projecting flaps of test thought to be lateral organs in these aspicular colonies suggest that they also may have a role in anchoring the thorax in the test.

Didemnum elongatum Sluiter, 1909 (Figs 83C-E, 169B; Pl. 8H)

Didemnum elongatum Sluiter, 1909: 66.

NEW RECORDS. Western Australia (NW of Port Hedland, WAM 79.89 125.93). Queensland (Tydeman Reef northern Great Barrier Reef, QM G302906).

PREVIOUSLY RECORDED. Indonesia (Sluiter, 1909, syntypes ZMA TU444, TU445).

COLONY. Colonies are thin (to 3mm) tough to hard encrusting sheets, white to cream in preservative, although some dark pigment

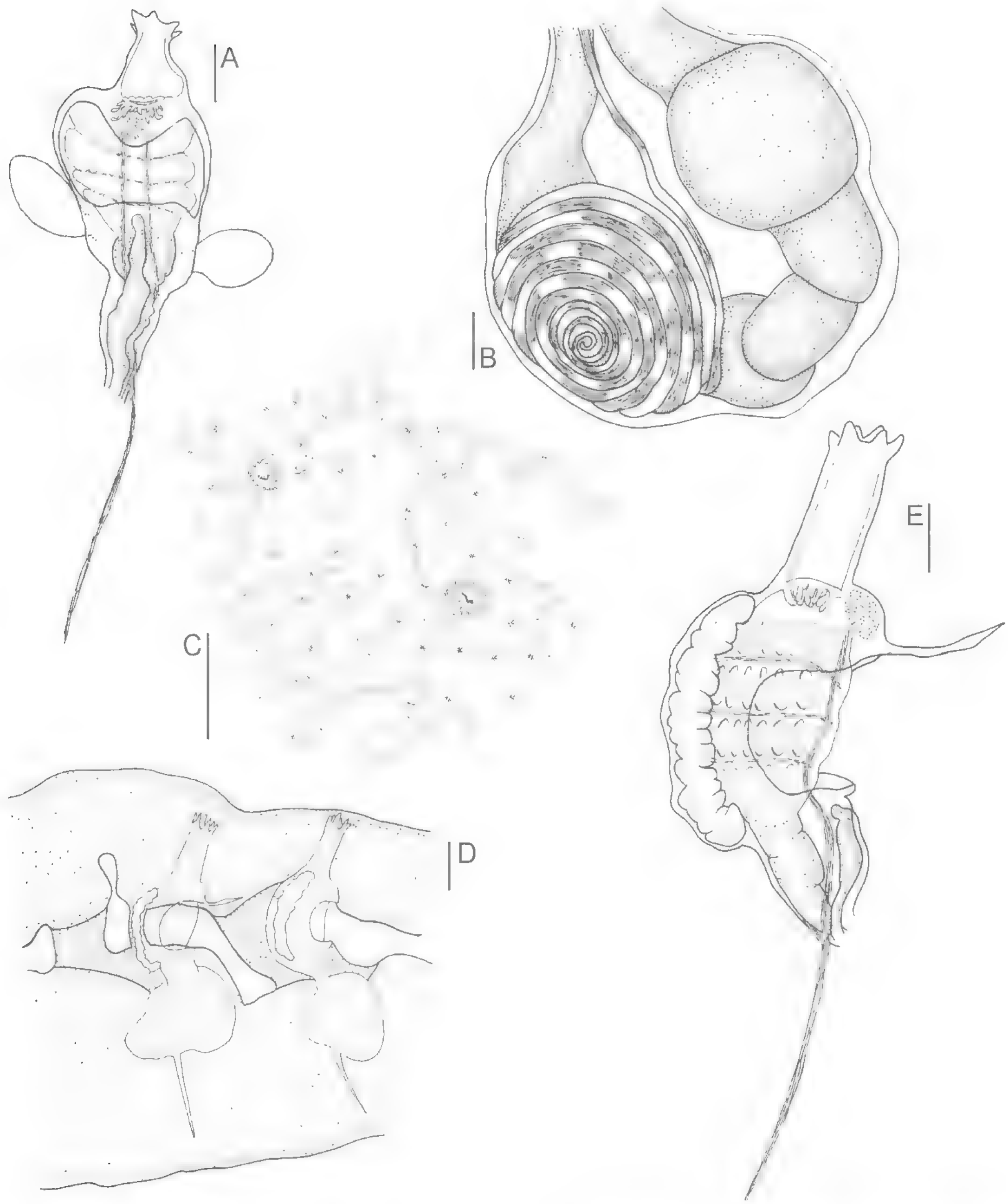


FIG. 83. A, B, *Didemnum effusium* sp. nov. (QM G10139) – A, thorax from dorsal surface showing projecting lateral organs; B, abdomen. C–E, *Didemnum elongatum* (C, WAM 79.89; D,E, WAM 125. 93) – C, part of colony surface; D, semidiagrammatic vertical section through colony; E, contracted thorax. Scales: A,B,E, 0.1mm; C, 1.0mm; D, 0.2mm.

granules are mixed with spicules in the upper layer of one specimen (WAM 79.89). Generally the surface is smooth, but occasionally some spicule filled papillae of various sizes are irregularly distributed (ZMA TU444). Spicules line the margins of stellate branchial apertures which, in some parts of the colony, are arranged in double series along each side of circular common cloacal canals that surround solid stands of test which protrude slightly from the upper

surface. Spicules are present throughout the colony, although they are less crowded at thorax level (i.e. the upper third of the colony) than they are at abdominal level. The primary common cloacal canals that surround clumps of zooids or zooid-free test are deep and extend posterior to the zooids and also are continuous with thoracic cavities that penetrate amongst the zooids in a clump, isolating the thoraces in a strip of test that connects the thick surface layer to the middle layer of test.

Spicules, to 0.08mm diameter, are of two sorts, some with 9–11 conical pointed rays in optical transverse section, and others with short rounded rays. Occasionally the conical rays have chisel-shaped, or bifid, or trifid comb-like tips. The only colour notes on living specimens are from Tydeman Reef (QM G302906), said to be pale pink-purple-white.

ZOOIDS. Zooids are robust, about 1.5mm long and firmly fixed in the test. Conspicuous columnar epithelial cells project from the surface. The long cylindrical branchial siphon is about half the length of the thorax, and is associated with the thick surface layer of test. Six sharply pointed lobes project from the rim of the siphon. An atrial tongue from the upper rim of the opening is inserted into the test over the primary cloacal canal. A spherical clump of spicules from the lateral organ is along the edge of the thoracic test sheath. A tapering retractor muscle extends from the upper part of the long oesophageal neck. The long, narrow branchial sac has 8 long, rectangular stigmata in the anterior row, 7 in the second and 6 in the last 2 rows. The oesophageal neck is long (about the same length as the thorax, and the stomach, duodenum, posterior stomach and proximal part of the rectum are in an almost vertical loop at the distal end of the abdomen. A large dome-shaped, undivided testis has 6 coils of the vas deferens around it. Larvae are not known.

REMARKS. The species is distinguished by its 3-dimensional cloacal system, long branchial siphon, long oesophageal neck, atrial lip and the 2 different types of spicule. *D. tonga* has a long branchial siphon and oesophageal neck, but lacks an atrial lip; and, although it has 2 sorts of spicules, they have fewer rays, conical-rayed spicules are not present and some have long, rod-like rays unlike the rounded stumpy rays in the present species. The two sorts of spicules in the present species resemble some in *D. moseleyi*, although the latter species also has globular ones (without protruding rays). Further, *D. moseleyi* has more coils of vas deferens, a shorter branchial siphon and oesophageal neck, a two-dimensional cloacal system, and it lacks an atrial lip.

Didemnum guttatum Monniot & Monniot, 1996 from Indonesia and Papua New Guinea has a long branchial siphon but spicules with fewer, broader and shorter rays and a thoracic common cloacal system. *D. ossium* has lobed colonies (with terminal common cloacal apertures) rather than sheet-like ones, smaller spicules, more numerous vas deferens coils and although its branchial siphon is conspicuous it is tulip-shaped and not nearly as long as the present species.

The temperate *D. macrosiphonium* has a similar but shorter branchial siphon, and large zooids along each side of circular common cloacal canals. The spicules also are similar but only half the size.

Didemnum etiolum Kott, 1982
(Figs 84A-D, 170G)

Didemnum etiolum Kott, 1982a: 104; 1998: 82. Monniot, 1995: 307.

DISTRIBUTION. NEW RECORDS. Queensland (Capricorn Group, QM GH957, GH3029, G301528, G302203).

PREVIOUSLY RECORDED. Queensland (northern Great Barrier Reef – syntypes QM GH247, QM GH272 Kott, 1982a). Coral Sea (Chesterfield Reef, Monniot, 1995). New Caledonia (Monniot, 1995). Philippines (QM GH459 Kott, 1982a).

COLONY. Colonies are always particularly small, soft and inconspicuous plates to 1cm long, but usually less. A central cloacal aperture protrudes slightly from the centre of the upper surface. Zooids are in a circle around the periphery of the colony forming slight elevations in the upper surface. The surface layer of test is thin, and separated from the basal test (in which abdomina are embedded) by a thoracic cloacal cavity. Spicules are found throughout the test, although they are most crowded in the basal layer of test. They are up to 0.045mm diameter, with 5–7 long, narrow, tapered conical rays in optical transverse section. Some dark pigment cells are present in the surface layer of test and large spherical (test) cells lying free in the colony surround the zooids.

ZOOIDS. Zooids are particularly small (to 0.5mm long). The branchial siphon is moderately long with shallow lobes on its rim. The atrial aperture is transverse, across the dorsum of the branchial sac about halfway down the thorax. A fine retractor muscle projects from the posterior end of the thorax. Depending on the condition of

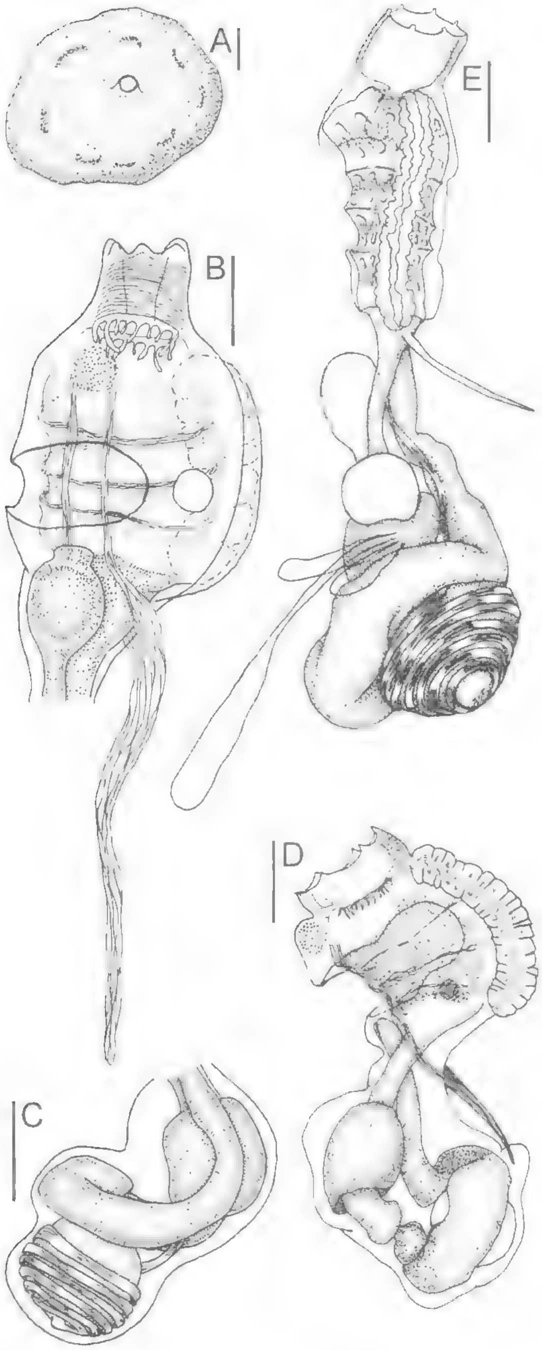


FIG. 84. A–D, *Didemnum etiolum* (A,C, QM GH459; B,D, QM GH3029) – A, colony from above showing protuberant central common cloacal aperture after Kott (1982a); B, thorax right dorso-lateral aspect; C, gut loop and testis from left; D, contracted zooid. E, *Didemnum flavoviride* (QM G3477) – E, zooid from ventral surface showing 2 buds, stolonic vessels. Scales. A, 0.2mm; B–E, 0.1mm.

the thorax, a large lateral organ is opposite the third or fourth row of stigmata on each side of the thorax. Four or 5 stigmata per row are in the branchial sac. The distal end of the gut loop is flexed ventrally. Six coils of the vas deferens surround the outside of the undivided, almost spherical testis (QM GH3029).

Larvae (Monniot, 1995) have a trunk 0.4mm long, 3 antero-median adhesive organs, 4 pairs of ectodermal ampullae and *Prochloron* embedded in the larval test, leaving clear windows without the embedded symbionts in front of the adhesive organs and over the cerebral vesicle. The tail is wound two-thirds of the way around the trunk.

REMARKS. The species has spicules like *D. cuculliferum* but is distinguished by its small, soft colonies and the embedded *Prochloron* which confers the green colour to the living colony. It is one of only 3 known species of *Didemnum* with an apparently obligate symbiosis with embedded *Prochloron*, the others being *D. flavoviride* Monniot, 1995 and *D. verdantum*. *D. molle* (Herdman, 1886) has *Prochloron* in its cloacal cavity and *D. guttatum*, *D. herba*, *D. viride* and possibly *D. poecilomorpha*, have cyanophyte symbionts in the test. *D. flavoviride* has equally small colonies but different spicules, sparsely distributed and only in the upper half of the colony, and its green colour persists in preservative. *D. verdantum* appears to be most closely related to the present species, having similar spicules and free dark test cells around the zooids but it differs in its larger sheet-like colonies, more vas deferens coils, and larvae with more ectodermal ampullae. The spherical, dark cells surrounding the zooids are similar to those in some specimens of *D. viride* and other species (see Glossary, **haemocoel**).

Didemnum flavoviride Monniot, 1995
(Figs 84E, 166B)

Didemnum sp. ('diminutum') Parry & Kott, 1988: 150.
Didemnum flavoviride Monniot, 1995: 308.

NEW RECORDS. Queensland (Heron I., QM GH3477, GH3877; Britomart Reef, QM GH381).

PREVIOUSLY RECORDED. Queensland (Heron I. – Parry & Kott, 1988). New Caledonia (Monniot, 1995).

The species has been recorded to 12m. It is cryptic, and many colonies are found crowded together around the base of coral skeletons with other species of cryptic didemnids, usually with green prokaryotic symbionts.

COLONY. The flat-topped cushion-like colonies are minute, to about 2mm thick and 5mm long. They come to a point (by which they are attached) basally. In life these minute colonies are green

and translucent. In preservative the green persists, the colonies look fluffy and are firm and slippery. Spicules are sparse in the surface test but become more crowded in the middle of the colony — around the zooids. They are absent from the basal test beneath the fairly shallow thoracic cloacal cavity. *Prochloron* and red rod-shaped cyanophytes are embedded in the test (Parry & Kott, 1988), but are not in the common cloacal cavity. Spicules are up to 0.03mm diameter, burr-like with crowded cylindrical, flat-ended to round-tipped rays.

ZOOIDS. Zooids are small with the thorax (0.25mm long) about half the length of the abdomen (0.04mm). A retractor muscle projects from the posterior end of the thorax. A small lateral organ is in the centre of each side of the thorax between the second and third rows of stigmata. Six rounded to pointed branchial lobes fringe the rim of the short siphon. The atrial aperture is a large, sessile opening around the middle of the dorsal surface of the thorax. Five stigmata are in the first 2, and 4 in the last 2 rows of the branchial sac. The oesophageal neck is long and the distal part of the gut loop is rounded and bent ventrally. Two or 3 vascular stolons with conspicuous terminal ampullae project from the ventral side of the gut loop into the test. An undivided testis is behind (or dorsal to) the flexed part of the gut loop, with 7 coils of the vas deferens around it. Larvae are almost spherical, the trunk about 0.5mm long. Larval structure is obscured by embedded plant cells in the larval test, plant cells being absent only over the cerebral vesicle and adhesive organs. In the New Caledonian material 4 ectodermal ampullae are along each side of the 3 antero-median adhesive organs and a blastozooid is reported (Monniot, 1995). Larvae are in QM GH3477 collected in April from Heron I.

REMARKS. Colonies are small, like those of *D. etiolum*. Both species have *Prochloron* embedded in the test, but their spicules are different, *D. etiolum* having stellate spicules with relatively few rays. Other small species with obligate symbiotic *Prochloron* embedded in the test are *Trididemnum miniatum*, *T. nubilum*, *T. clinides* and *T. paraclinides*. In addition to the generic difference from the present one, all have slightly larger colonies, larger zooids and generally larger spicules. Only *T. miniatum* has burr-like spicules similar to those of the present species but they are smaller (to 0.02mm diameter). *D. poecilomorpha* also has small colonies and green plant cell symbionts embedded in the test, but they are cyanophytes rather than *Prochloron*.

In larvae from New Caledonia, Monniot (1995) observed that the blastozooid develops early, before the branchial sac of the oozooid was fully formed. Unfortunately the larval structure of the Australian material was obscured by the plant cells in the larval test.

Didemnum fragile Sluiter, 1909
(Figs 85, 166A; Pl. 9A)

Didemnum fragilis Sluiter, 1909: 56 (part, ZMA TU446.1 part B). Monniot & Monniot, 1987: 30 (part, specimens with 6 vas deferens coils); 1996: 153.
Didemnum proliferum Kott, 1981: 171.
Didemnum candidum: Hastings, 1931: 94 (part, specimens with burr-like spicules). Tokioka, 1967: 62 (part, specimens with spherical spicules and an undivided testis follicle).

NEW RECORDS. Western Australia (Kimberley, WAM 791.91). Queensland (Capricorn Group, G308105, G308119, G308124, G308159, G308163, G308254, G308256, G308280; Swain Reefs, QM G308359, G308365-6, G308401, G308415, G308432; Bowden Reef, QM GH5354). Timor Sea (Ashmore Reef, WAM 520.92).

PREVIOUSLY RECORDED. Queensland (Low Is – Hastings, 1931). West Pacific (Indonesia – lectotype ZMA TU446.1B Sluiter, 1909; French Polynesia – Monniot & Monniot, 1987; Palau Is – Monniot & Monniot, 1996; Fiji – Kott, 1981).

COLONY. The colonies are thin investing sheets or small cushions to about 1cm in greatest dimension, with rounded margins. In life, colonies are rose pink[R] or salmon colour[R] with rose-red[R] or carmine to yellow zooids. Irregular rose-red[R], vermilion[R] or dragon's blood red[R] pigment cells are sometimes scattered in the surface test, and in preservative these appear as a dirty brown discolouration of the white colony. Spicules are crowded throughout the colony, although usually (QM G308105, G308159, G308163) vesicles interrupt them in the surface, sometimes making the spicule layer appear slightly areolated with spicules in little clumps and rows. Branchial apertures are surrounded by crowded spicules. Occasionally these are absent from a small area around each aperture although they invariably outline the margin of the opening.

The thoracic common cloacal cavity is extensive and often clumps of abdomina project up into the floor of the cavity . Thoraces cross the cavity each with an individual ventral test sheath.

Spicules are globular or burr-like, to 0.04mm in diameter, with narrow, radially arranged,

compact or rather loose flat- or chisel-tipped rod-like rays.

In a colony from the Capricorn Group (QM G308159), long ridges containing zooids and thoracic cloacal cavities are separated from one another by depressions of the thin layer of surface test over deep primary cloacal canals and some parts of the surface are raised into blister-like protuberances containing 1–6 zooids. Spicules are sparse in the surface of these blisters, and absent internally.

ZOOIDS. Zooids are small, about 0.8mm long. The retractor muscle extends free of the zooid from a short distance down the oesophageal neck. Six pointed lobes surround the branchial aperture. The atrial aperture is wide, exposing most of the dorsal part of the pharynx directly to the cloacal cavity. An atrial lip is not present.

The branchial sac has 8 stigmata in the 2 anterior rows, and slightly fewer in the posterior rows. The gut loop is long, but the post-pyloric part of the loop is bent ventrally, up against the anterior part. A large, egg-shaped testis, its long axis projecting from the zooid, is beneath the flexed part of the gut loop. Six coils of the vas deferens are around its outer half only. Stolonic vessels project from the ventral concavity of the gut loop.

Larvae in colonies collected from Heron I. in March (QM G308105, G308124) and the Kimberley in August (WAM 791.91), have a trunk 0.5mm long. Four lateral ampullae are along each side of the 3 antero-median adhesive organs and the tail is wound three-quarters of the way around the trunk.

REMARKS. Monniot & Monniot (1987) re-examined the types of *D. fragile* from the *Siboga* collection (Sluiter, 1909), and reported that they corresponded exactly in both colony, zooids and larvae to the French Polynesian specimens. However, Sluiter's syntypes re-examined in the present study are not all conspecific. Even in one specimen lot (ZMA TU446.1) there are 2 different species. One (ZMA TU446.1A) has evenly spaced zooids (not in clumps) with the thoraces crossing the shallow horizontal cloacal cavity independently and globular spicules with crowded rays to 0.06mm in diameter that most closely resemble the spicules of *D. precocinum*. The atrial lip characteristic of the latter species and the testis and vas deferens coils were not detected in the Indonesian specimen, but they may be obscured as the zooids are contracted. The other specimen

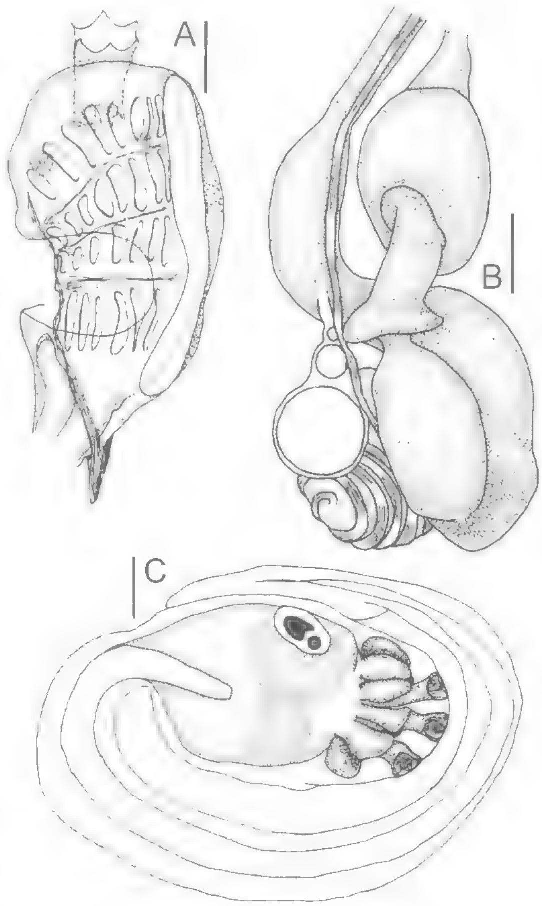


FIG. 85. *Didemnum fragile* (A, QM G308124; B, WAM 791.91; C, QM G308105) – A, thorax; B, gut and gonads; C, larva. Scales: 0.1mm.

(ZMA TU446.1B) is here identified as the lectotype of the present species. It has a rather fleshy colony with well-spaced small (to 0.035mm diameter) spicules with relatively loose rays as reported by Sluiter (1909). Zooids are clumped together with deep cloacal canals around each clump that extend the full length of the zooids. Larvae, being incubated in the basal test, appear to be liberated through the cloacal cavity. The larval trunk is about 0.9mm long with 4 pairs of lateral ampullae. Although it conforms with most aspects of Sluiter's description, it does not seem as brittle as it was reported to be, and possibly Sluiter confused the 2 specimens. Another specimen assigned to this species (ZMA TU446.2) also has globular spicules, usually to

0.03mm diameter, although a few are 0.04mm. It is hard and brittle, its cloacal cavity is thoracic but limited and, although there are 5 coils of the vas deferens, they coil around 2 male follicles (see *D. recurvatum* Sluiter, 1909).

The newly recorded specimens have a shorter larval trunk, but spicules of the same size and form, 6 vas deferens coils and an undivided testis as in the lectotype. Spicules reported for *D. fragile*: Monniot & Monniot, 1987 are like those of the lectotype, and the length of the larval trunk (0.9mm) also is the same. Although the zooid (Monniot & Monniot, 1987, fig. 8F) has only 6 vas deferens coils like the present specimens, the latter authors reported the number to be 7–10. This range is too great to be intraspecific, and more than a single species may be involved. Unfortunately it is not known whether or not the relatively large larvae these authors describe come from colonies with greater or lesser numbers of vas deferens coils. Zooids from Low Is (Hastings, 1931) also have 6 coils of the vas deferens although Hastings (like Kott, 1981) had recorded only 5.

D. proliferum Kott, 1981 from Fiji has the same range in colour, spicules of the same size and shape, 8 stigmata per row, and the same shaped testis, with vas deferens around the outer half. Further the larva of *D. proliferum* is the same size (0.5mm long) and form as the newly recorded specimens.

D. parau Monniot & Monniot, 1987 also resembles the present species. It has similar spicules, although its larval trunk is even shorter (0.370mm) and it has 7 coils of the vas deferens.

D. albopunctatum has similar spicules although they tend to be more compact and smaller (seldom more than 0.03mm in diameter). Other differences from *D. fragile* are discussed above (*D. albopunctatum*, Remarks). *D. precocinum* has similar but more compact and slightly larger spicules, an atrial lip, and a larger larva with blastozooids and more ectodermal ampullae.

The significance of the blister-like protuberances on part of a colony surface (QM G308159) is not understood. They resemble blisters in *D. apuroto* Monniot & Monniot, 1987, but the spicules of the latter species are stellate, with conical or flat-ended rays, 9–11 in optical transverse section. These protuberances may be abnormal and not of taxonomic significance.

Didemnum fragum sp. nov.
(Figs 86, 169H; Pl. 9B)

Leptoclinum jugosum Herdman & Riddell, 1913: 886 (part), AM G12208 Z1288 – 90 Z1305.
Didemnum lambitum: Kott, 1954: 164; 1962: 317 (not Bracebrige Wilson's colony); 1972a: 18; 1976: 70; 1998: 82.
Not *Didemnum lambitum* Kott, 1972c: 249 (< *D.complexum*).

TYPE LOCALITY. South Australia (St Vincent Gulf, Nora Creina Bay, coll. AIMS Bioactivity Group 20.2.89, holotype SAM E2680; Franklin I. intertidal rock pools, NW of W. Island, coll. W. Zeidler, P. Aerfeldt et al., 24.2.83, paratype SAM E2832; Eyre Peninsula, Boston I., Kangaroo Reef off Maria Point, large boulder reef, rubble, kelp and sparse *Posidonia*, sand 3-8m, coll. W. Zeidler and K.L. Gowlett Holmes 17.2.88, paratype SAM E2838; Pt. Souttar, southern Yorke Peninsular 4m, coll. AIMS Bioactivity Group 8.2.89, paratype QM GH5438).

FURTHER RECORDS. South Australia (Nuyts Archipelago, SAM E2675, E2833). Victoria (Bass Strait, MV F70260; Western Port, MV68754).

PREVIOUSLY RECORDED. South Australia (St Vincent Gulf – SAM E2681 Kott, 1972a). Tasmania (eastern coast – AM Y1519 Kott, 1954). Victoria (Port Phillip Bay – Kott, 1976). New South Wales (Off Coffs Harbour, Manning Bight, off Cape Three Points – AM G12208, Z1288-90, Z1305; Herdman & Riddell, 1913; Kott, 1962).

COLONY. Colonies are firm vertical or lopsided cones, often slightly laterally flattened, either single or 2 or 3 lobed, to 6cm high. The upper surface narrows to a sessile terminal or sub-terminal common cloacal aperture. The lower surface is flattened and fixed to the substrate, or a short stalk spreads into a thin holdfast over the substrate. In all colonies a thin superficial layer of bladder cells overlies an even, opaque layer of spicules at the level of the branchial siphons. Spicules become less crowded through the remainder of the test which is translucent, and sometimes quite soft. Spicules are clumped together in the siphonal linings, where they are seen as small white points in the surface. The branchial apertures are very evenly distributed. The common cloacal cavity is 3-dimensional, with deep canals around clumps of zooids extending into the sometimes extensive posterior abdominal spaces separating the zooid-bearing surface layer of the colony from the central test core (of the upright lobes) or the basal test (of the flat parts of the colony). More restricted spaces penetrate amongst the zooids at thorax level.

Colonies are orange/beige to pink in life but white in preservative.

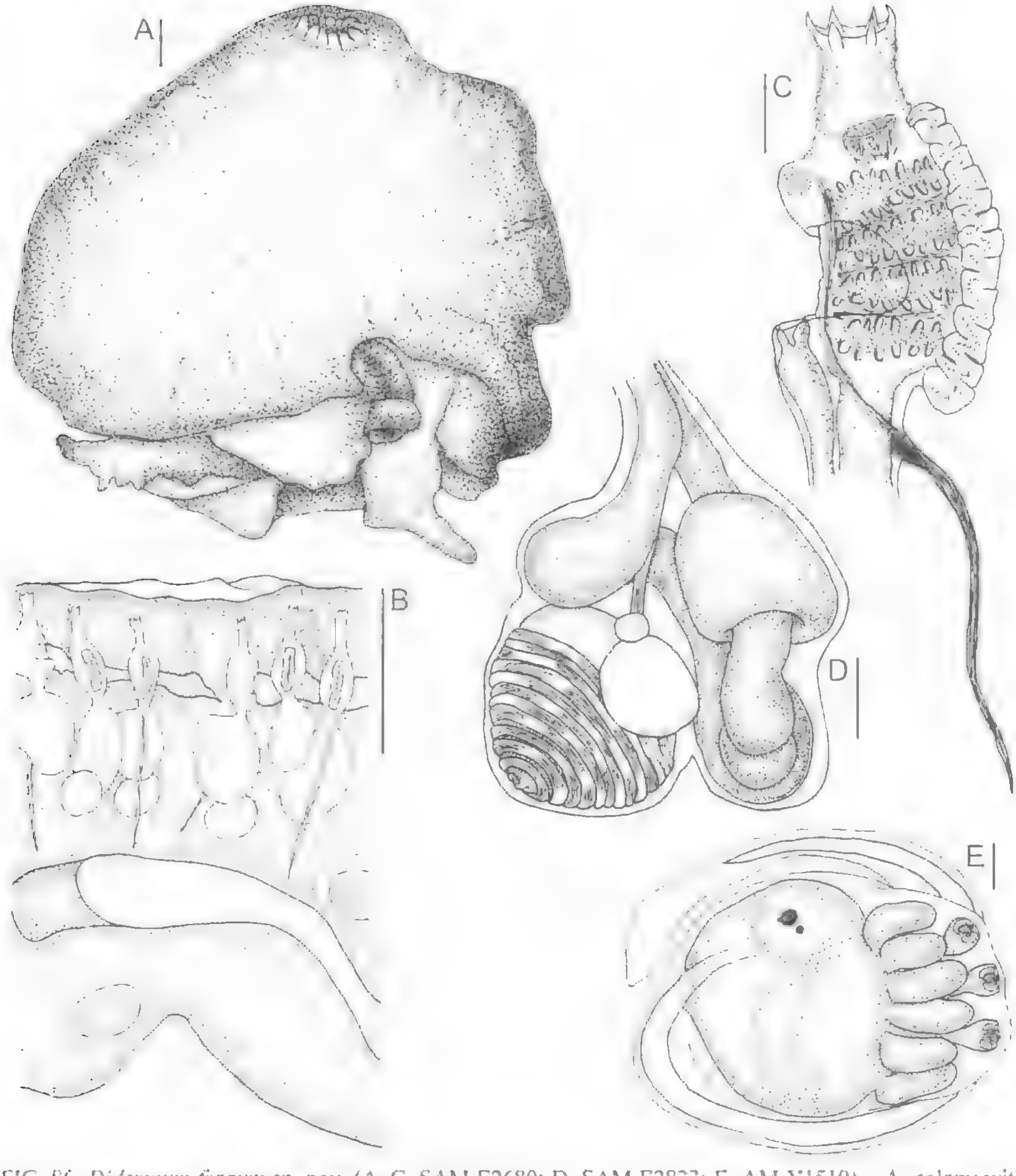


FIG. 86. *Didemnum fragum* sp. nov. (A–C, SAM E2680; D, SAM E2833; E, AM Y1519) – A, colony with terminal common cloacal aperture; B, semidiagrammatic vertical section through part of colony showing thoracic and posterior abdominal cavities; C, thorax; D, gut loop and gonads; E, larva. Scales: A, 0.2mm; B, 1.0mm; C–E, 0.1mm.

Spicules are stellate to 0.07mm diameter, with 9–13 sharply pointed, conical rays. Ray length/spicule diameter ratio is about 0.2.

ZOOIDS. Zooids are small (to about 1mm long) and crowded perpendicular to the surface. Round-tipped columnar cells seen in stained preparations are invariably present projecting from the ectoderm, and may be the means by which the zooids are firmly fixed in the surrounding test, from which they are removed with difficulty. The branchial siphon is long and cylindrical (almost half the length of the

contracted thorax) with 6 long, sharp points around the rim of the aperture. The atrial aperture is a relatively restricted sessile opening around the middle part of the branchial sac. It has circular muscles around it. The body wall is not especially muscular, the usual longitudinal fibres in the parietal body wall join the paired dorsal pharyngeal muscles to form the fine tapering retractor muscle that projects from about the middle of the long oesophageal neck and extends straight to the roof of the posterior abdominal common cloacal cavity.

Six stigmata were detected in the anterior row of some zooids, although generally these were too contracted for accurate determination. The post-pyloric part of the gut loop is flexed ventrally. The large conical to top-shaped undivided testis is against the posterior end of the loop, its apex sometimes abruptly reducing in diameter to contrast with the broad, basal part. Twelve tight vas deferens coils surround the whole depth of the testis.

Large oval, yellow eggs (to 0.6mm long) are in the abdomina and in the basal test of the newly recorded colony (QM GH5438). They are a similar size to the eggs in the colony from Tasmania (Kott, 1954) in which larvae with a large larval trunk (to 0.9mm long) have 6 finger-like ectodermal ampullae at each side of the adhesive organs.

REMARKS. *D. pecten* and *D. pellucidum* have similar colonies and zooids with long branchial siphons. *D. pecten* has short cylindrical colony lobes with single terminal common cloacal apertures, shorter branchial siphons, 9 coils of the vas deferens and smaller larvae (0.5mm larval trunk). *D. pellucidum* generally has more colony lobes and long ridges that may fuse with one another, larger spicules than the present species, and a particularly large larval trunk with 12 ectodermal ampullae per side. *D. sucosum* (>*D. spongioides*: Kott, 1962, part, from Oyster Bay Tasmania) has terminal cloacal openings, spicules crowded at the surface but sparse elsewhere. It is distinguished from *D. fragum* by its larger spicules (to 0.125mm diameter), 4 pairs of larval ectodermal ampullae (rather than 6) and a large larval trunk (to 0.9mm long), as well as the long branching stalks (3 – 7cm) that support the fleshy heads that comprise the colonies. The smaller colonies from Rottnest I. assigned to *D. spongioide* by Kott, 1962 (AM U3945) have been re-examined and found to be specimens of the tropical *D. roberti* Michaelsen, 1930 which has similar, cloacal systems and spicule distribution to the present species, although its zooids are larger and more muscular, and the spicules have fewer and more attenuated pointed rays. The colony of the present species (and of *D. lambitum*) resembles that of *Polysyncraton jugosum*, but the species are separated by generic characters and by different spicules.

Specimens from the east coast of Tasmania assigned to *D. lambitum* by Kott (1954) have similar colonies, spicules and zooids to the newly recorded material and are considered conspecific.

D. lambitum (Sluiter, 1900) from New Zealand (type localities Waitangi and Chatham I.) is known from other New Zealand locations around the North and South Islands (Michaelsen 1924; Kott, 1971; Millar, 1982) and newly recorded specimens from Port Pegasus (QM G9620). Although the colony, zooids and spicule form and distribution are similar to the present species — both having a maximum of about 6 stigmata per row, a relatively restricted sessile atrial aperture with circular muscles, a tapering retractor muscle of varying length and a larval trunk about 0.9mm long — there are consistent differences between the two. Examination of the newly recorded material has demonstrated that the New Zealand species has spicules with only 9 to 11 rays in optical transverse section, a relatively short branchial siphon, longer stigmata, 10 (rather than 12) coils of the vas deferens a beehive-shaped (rather than conical) testis, and 4 (rather than 6) larval ectodermal ampullae per side. Although it has been reported that this species has separate male and female phases, both ovaries and testes are present in this colony and often in the same zooids. However, the species may be protygynous.

Specimens questionably referred to *D. lambitum* by Millar (1982) with spicules throughout the colony, smaller larva and larger atrial aperture do not belong to this species.

Nevertheless, it is not impossible that the differences detected between this temperate Australian species (with a range from Nuyts Archipelago to the central NSW coast) and the New Zealand species represent intraspecific variation. Nor can their conspecificity be ruled out on geographic grounds. Some western Pacific tropical species include North Island (New Zealand) in their range. Some temperate taxa also are recorded from around the south east of Australia and New Zealand viz.: *Dumus areniferus* (Ritterellidae Kott, 1992a), *Euclavella*

claviformis (Pycnoclavellidae Kott, 1990a), *Botryllus stewartensis* and the *pachydermatina* group of *Pyura* (Botryllidae and Pyuridae respectively and are possible Gondwanan components of the Australian-New Zealand fauna (see Kott, 1985).

Didemnum fucatum Sluiter, 1909
(Figs 87, 172A; Pl. 9C,D)

Didemnum fucatus Sluiter, 1909: 47.

NEW RECORDS. Queensland (Heron I., QM G302980, G302996; Deloraine I., QM GH5753; Lizard I., QM G302033).

PREVIOUSLY RECORDED. Indonesia (holotype ZMA TU448, Sluiter, 1909).

COLONY. Colonies are extensive, soft, encrusting sheets, some fleshy with rounded ridges and lobes projecting from the surface which may branch and coalesce to form a large trabecular mass in some places (QM G302980). Other colonies are fleshy slabs with a smooth surface. A conspicuous spicule-free superficial layer of bladder cells contains brown pigment. Large common cloacal apertures are spaced about 1cm apart around the margin of the colony and are randomly scattered over the surface. They have spicule-free rims and are brown and conspicuous. Spicules are absent from the test over the primary common cloacal canals, which, as a consequence, appear as a brown network around whitish oval to circular areas where the white spicules in each clump of zooids show through the surface test. The circular primary common cloacal canals extend the full depth of the zooids separating them into clumps. These primary canals expand into posterior abdominal spaces, interrupted by single connectives anchoring each clump to the basal layer of the test. Thoracic cavities penetrate amongst the zooids in each clump. Zooid openings are along each side of the primary cloacal canals as well as in the centre of each clump of zooids.

Spicules are fairly evenly but sparsely distributed in the middle layer of the colony beneath the thoracic common cloacal cavities and in the test in and around each clump of zooids but they are rare elsewhere. They are large, to 0.1mm in diameter with 9–11 long, pointed rays in optical transverse section. Rays vary in length. Ray length/spicule diameter ratio is up to 0.4.

In life, the newly recorded specimens appear black to bottle- or olive-green or brown with the reddish to brown (ferruginous) zooids clearly seen through the greenish, translucent to transparent test. In preservative colonies are brown and the test is translucent. In some colonies large brown spherical bodies are in some parts of the test. Eggs are reddish and translucent.

ZOOIDS. Zooids are about 1.3mm long, with the abdomen small, about one-third of the length of the thorax. The branchial aperture, on a small siphon, has 6 narrow pointed or tongue-like lobes around the rim. The branchial siphon is small. The atrial aperture is a small, sessile opening, on the posterior third of the dorsal border of the thorax. It opens directly into the cloacal cavity that surrounds each group of zooids. It is a circular or occasionally transverse opening (depending on the condition of the zooid). Fine transverse muscles cross the dorsal line of the zooid anterior to the atrial aperture, fine longitudinal muscles extend down each side of the parietal thoracic wall and fibres from the most dorsal longitudinal bands join a sphincter around the atrial aperture. Posteriorly the longitudinal muscles join an annular muscle ring around the oesophageal neck of the zooid which appears to constrict the neck. Paired dorsal longitudinal pharyngeal muscles along each side of the dorsal mid-line of the pharynx are strap-like but delicate. There is no retractor muscle. A circular lateral organ is in the middle of each side of the thorax opposite the interspace between the first and second rows of stigmata. The stigmata are large and oval, 9 in the first row reducing to 7 in the last 2 rows. The short, open gut loop has the usual subdivisions (stomach, long duodenum, small round posterior stomach, and a long rectum with a constriction surrounded by tubules of the gastrointestinal gland halfway along its length). A single vascular stolon projects from the concave (ventral) side of the gut loop.

Mature dome-shaped testes each surrounded by 5 coils of the vas deferens, are present in the holotype and in QM G302980. Embryos and larvae are present in the holotype. The larvae are present just below the upper surface of the colony and are very likely liberated directly through the surface test. Larvae are large, the larval trunk from the holotype being about 1.1mm long. Four long finger-like lateral ampullae are along each side of the 3 antero-median adhesive organs. A large circular lateral organ is invaginated into the parietal body wall on each side of the larval thorax. A blastozooid is not present. The oozooid is well-developed with otolith, ocellus, vertical gut and 3 rows of stigmata in the branchial sac, the tail is wound only two-thirds of the way around the trunk.

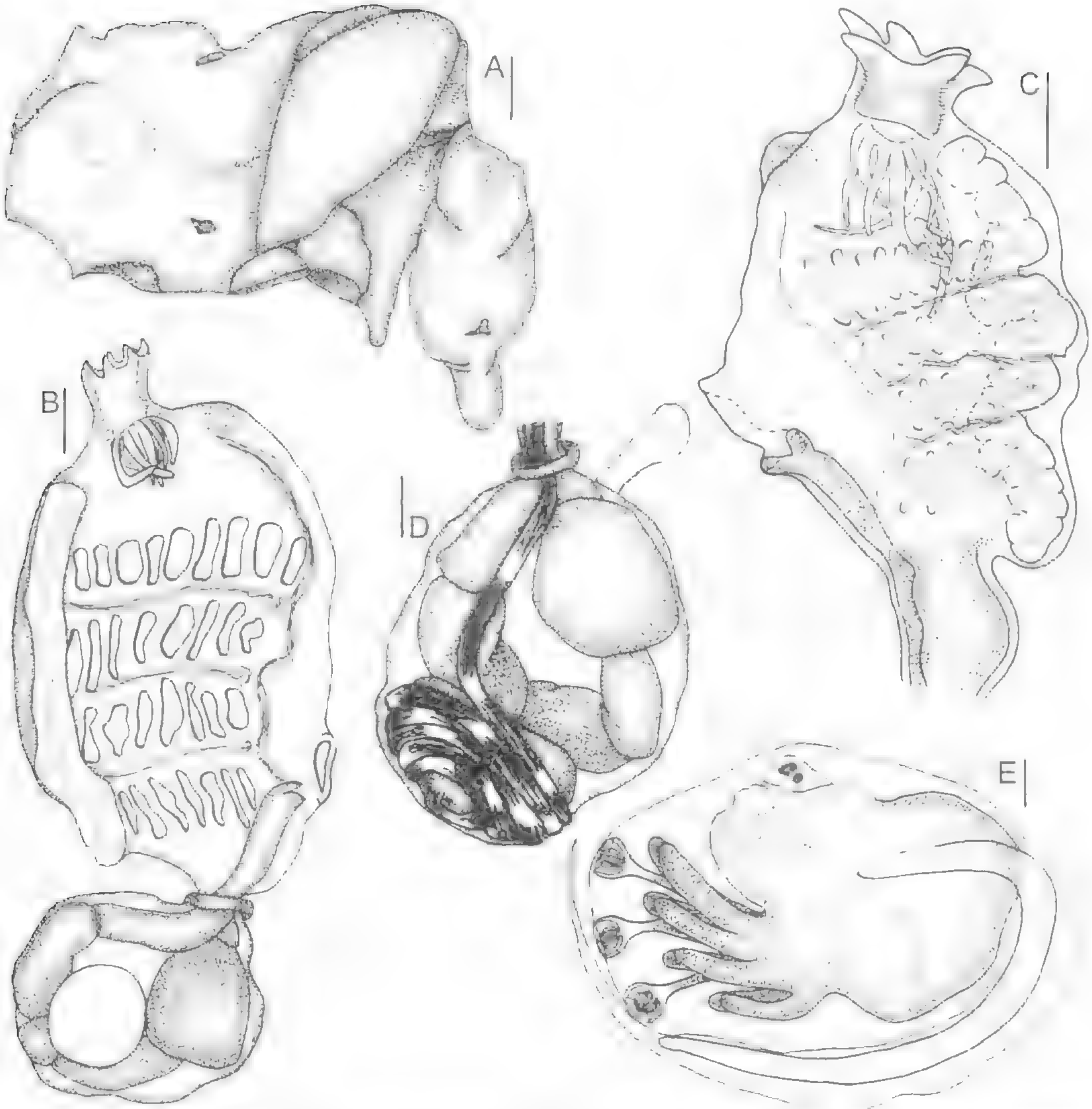


FIG. 87. *Didemnum fucatum* (A,B,D, QM G302980; C, QM GH5753; E, ZMA TU448) – A, colony; B, zooid; C, thorax; D, gut loop and testis; E, larva. Scales: A, 5.0mm; B–E, 0.1mm

REMARKS. This species is an unusual member of *Didemnum*. It differs from other *Didemnum* spp. in its posteriorly directed small, sessile atrial aperture which, although it is not as long, is possibly closer (morphologically) to the posteriorly directed atrial siphon of *Leptoclinides* than to the large openings of *Didemnum*, which expose a great part of the branchial sac directly to the cloacal cavity. The species also resembles *Leptoclinides* in the absence of the retractor muscle, although the oesophageal muscle that is present does not occur in *Leptoclinides*. However it occurs in other Didemnidae (*Diplosoma ata* Monniot & Monniot, 1987 and *Lissoclinum roseum* and *L. nebulosum*) and cannot be regarded as phylogenetically significant at genus level.

The spicules also are unusual in *Didemnum*, to some extent resembling those of *D. psammatode* and *Leptoclinides caelestis*. Again, this is not phylogenetically significant at genus level, although usually the spicules can be regarded as a species characteristic.

The anterior position of the lateral organ, which in *Leptoclinides* is on each side of the base of the

atrial siphon and in *Didemnum* between the third and fourth rows of stigmata, is unusual. Other characters such as zooid size and undivided testis are similar in *Didemnum*. Larvae are similar to those of many *Didemnum* spp., without blastozooids, with a simple vertical oozooid in the centre of the larval trunk and the lateral ampullae simple, finger-like, without balloon shaped tips or modified epithelium. The large lateral organs present in the larval thorax resemble those present in the larval thorax of *Atriolum robustum*.

Re-examination of the holotype has shown that Sluiter's (1909) description of the colony was generally accurate, although the unique nature of the zooid (with the small, posteriorly directed, sessile, atrial aperture, and absence of a retractor muscle) and the large spicules (with relatively few, and particularly long rays of variable length) were overlooked.

The atrial aperture of *D. cineraceum*: Monniot, 1995 is small, but is different from the restricted circular opening of the present species.

Didemnum fuscum Sluiter, 1909
(Figs 88, 171A)

Didemnum fuscum Sluiter, 1909: 52.
Not *Hypurgon fuscum* Oka, 1931: 287 (<*D. psammatode*).
Not *Didemnum (Didemnum) fuscum*: Tokioka, 1953: 192 (<*D. psammatode*).

NEW RECORDS. Western Australia (off Port Hedland, WAM 39.89;). Queensland (Capricorn Group, QM G302959, G308004, G308024, G308103, G308108, G308150, G308153, G308238, G308240, G308262-4, G308306). Timor Sea (Ashmore Reef, WAM 203.87).

PREVIOUSLY RECORDED. Indonesia (Sluiter, 1909).

COLONY. Colonies form encrusting sheets, to about 3mm thick. A continuous layer of spicules lines the branchial siphon and the test surrounding the stellate apertures and spicules are crowded throughout the colony. The common cloacal cavity is a horizontal space at the thorax level and abdomina are embedded in the basal test.

Living colonies are burnt carmine[R], claret brown[R], heliotrope purple[R], maroon purple[R] or magenta[R] with white borders (see QM G308004, G308150, G308153, G308262-4). They are dirty brown or cream in preservative and some diffuse brown pigment as well as minute pigment cells and spicules are mixed in the surface test. Dark brown or yellowish-brown zooids can be seen through the branchial apertures and sometimes brown larvae are being liberated to the exterior through the surface (QM G308004). Labels stain purplish-brown to pink. Large, brown spherical cells in the test amongst the spicules are also present around the zooids, apparently free of the test.

Spicules generally to 0.06mm, but occasionally to 0.09mm diameter, are crowded throughout the test. They have 7–9 long rays in optical transverse section. Rays usually are long, club-shaped with rounded tips and very rarely conical. Ray length/spicule diameter ratio is about 0.35.

ZOOIDS. Zooids are small, about 1mm long, with a small branchial siphon with 6-lobed aperture. In all the newly examined material, the atrial aperture is large, exposing the dorsal part of the branchial sac directly to the common cloaca. There is no atrial lip. Zooids are contracted in much of the available material. The number of stigmata could be determined accurately in only 2 colonies (QM G308153, G308262) where the anterior row had 6, the next rows 5 each and the last row 4 stigmata. The oesophageal neck is long. The fine retractor muscle projects into the test from about half-way down the oesophageal neck. A saucer-shaped lateral organ is on each side of the posterior one-third of the thorax.

The gut loop is vertical, the stomach spherical, the usual duodenum expanded at its distal end, the posterior stomach rounded, and the rectum expanded at its proximal end. A dome-shaped testis (flattened against the dorsal side of the post-pyloric part of the gut loop) has 9 coils of the vas deferens around its outer half. A large egg is present anterior to the testis

Larvae are present in specimens colected in March (QM G308004) and September (QM G308238). The larval trunk is only 0.4–0.45mm long. The tail is wound about two-thirds of the way around the trunk. An ocellus and otolith are present, 5 long, finger-like lateral ampullae are along each side of the anterior end of the trunk and a large horizontal ampulla projects forward from the middle of the trunk on the left side. The brown spherical cells found in the test also are present in the larval haemocoel.

REMARKS. Sluiter (1909) described colonies that were only 1.5mm thick with dark brown zooids. Although the newly recorded encrusting colonies are generally thicker than the type, the dark zooids and the long-rayed spicules are similar to those in the newly recorded material and comprise compelling evidence of their identity.

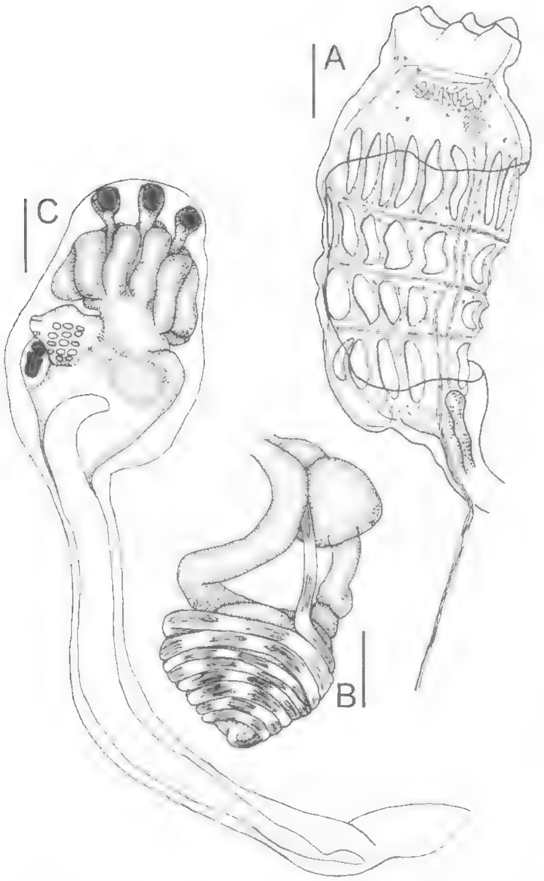


FIG. 88. *Didemnum fuscum* (A, QM G308262; B, QM G308108; C, QM G308004) – A, dorsal view of thorax; B, gut loop and testis; C, larva. Scales: 0.1mm.

D. sordidum and *D. spadix* (and other species, see Glossary, **haemocoel**) have similar large brown spherical cells free in the spaces surrounding the zooids and colouring the interior of the colony dark brown in preservative. *D. sordidum* also has a similar larval trunk only 0.45mm long but differs from the present species in its colour, more numerous and conspicuously conical spicule rays sometimes set in pentagonal bases, and generally smaller spicules. The South Australian species, *D. spadix* has spicules with conical rays more like those of *D. sordidum*. *D. candidum* has similar spicules, but their maximum diameter is only 0.06mm, larvae have only 4 pairs of lateral ampullae, zooids only 7 vas deferens coils and 8 stigmata in the anterior rows, and the species lacks the large brown sperical cells.

The spicules are in the group with long, sometimes rod-shaped, but often club-shaped rays that reduce in diameter toward the centre of the spicule as well as long blunt-tipped conical rays. *D. jedanense* Sluiter, 1909 also has this type of spicule with long rays but its spicules are smaller and have more numerous rays.

Didemnum grande (Herdman, 1886)
(Figs 89A–C, 172E; PL. 9G)

Leptoclinum albidum var. *grande* Herdman, 1886: 291.
Didemnum makropnous Sluiter, 1909: 54 (part, not ZMA TU461.2 < *D. perplexum* and TU461.6 < *D. stragulum*).
Not *Didemnum grande*: Van Name, 1918: 148. Kott, 1962: 325; 1998: 82.

NEW RECORDS. Western Australia (NNW Port Hedland, WAM 42.82). Queensland (Hervey Bay, QM G308475; Capricorn Group, QM G308162, G308286, G308298, G308498; Swain Reefs, QM G305607; Whitsunday Is, QM GH5365, G302939).

PREVIOUSLY RECORDED. Indonesia (syntypes *D. makropnous* ZMA TU461.3-5). Philippines (Cebu, holotype, slide BMNH 87.2.4.435pl. Herdman 1886).

COLONY. Colonies form large, thin sheets, 2–3mm thick. In preservative, a superficial spicule-free layer has brown pigment in minute, spherical cells mixed with bladder cells. Huge common cloacal apertures occur here and there over the surface of the colony at the junctions of deep primary cloacal cavities that extend the full depth of the zooids around clumps of zooids leaving only thin surface and basal test, respectively, as the roof and the floor of the cloacal cavities. The surface of the colony is depressed over these deep primary cloacal cavities around circular to oval elevations that protrude slightly from the upper surface. Sometimes zooids are partially embedded around these solid zooid-free oval areas of test. Sometimes abdomina are clumped together in the test connectives that join basal to surface test while thoraces are separated from one another by the secondary horizontal canals that penetrate the solid test at thorax level. Usually beneath the bladder cell layer the spicules are crowded throughout the test, causing it to be stiff and rigid. However, sometimes a layer of spicule-free test is just above the base and sometimes spicules are missing from the basal quarter of the colony thickness (QM G308498). Spicules are not present around the rims of the common cloacal openings which are dark with pigment. Branchial openings of the zooids on the surface of the colony are stellate, and the spicules, packed in the layer of test lining the inside of the siphons, outline the stellate openings.

Generally spicules are robust, up to 0.07mm diameter but occasionally larger ones (to 0.1mm diameter) are present. Nine to 11 and occasionally 7 acutely pointed conical rays are in optical transverse section. The ray length/spicule diameter ratio is 0.3 or more, the rays being moderately long.

Living colonies are brown and beige/tan, ecru-drab[R] and fawn[R] (QM G305607), or brown with blotches of yellow (QM G308298) with brown-rimmed common cloacal apertures (where spicules are absent) or purple (QM GH5365). The pigment is more intense in the depressions over the common cloacal cavities. Zooids are yellow. The white spicules packing the basal test are seen through the cloacal apertures. Green *Prochloron* is present in patches on the surface of the colony. In preservative the colonies are dirty looking brownish-white with brown pigment appearing more intense in the depressions over the primary cloacal cavities. Labels stain brownish yellow.

ZOOIDS. Zooids are robust overall, nearly 2mm long when relaxed. The branchial siphon is strong and cylindrical, with 6 small pointed projections around the rim. The atrial aperture is wide exposing most of the branchial sac to the cloacal cavity. An atrial lip is not present. A circular lateral organ is opposite the second row of stigmata at each side of the endostyle. A particularly long, fine retractor muscle projects toward the base of the colony from halfway down the oesophageal neck. The branchial sac is wide, with 11 stigmata in the anterior row, 10 in the second and third rows and 9 in the posterior row.

The gut loop is thick, and the post-pyloric distal part is bent back ventrally against the proximal part. A large dome-shaped testis follicle, with 7 coils of the vas deferens around it is against the ventrally flexed gut loop, and a smaller ovary is just anterior to it.

Larvae were taken from the basal test in March (QM G308498), September (QM G308298) and October (WAM 42.82, QM GH5365, G302939). The tail is wound almost all the way around the larval trunk, which is 0.6–0.7mm long. Four pairs of club-shaped lateral ampullae are present along each side of the base of the 3 antero-median adhesive organs. A horizontal lateral ampulla is on the left side of the trunk. An ocellus and an otolith are present. Sometimes circular plate-like ornaments are on the surface of the larval test (QM G308498). In other apparently identical larvae, these ornaments were not detected.

REMARKS. The large spicules with relatively long, sharply pointed, conical rays, wide thoraces, deep circular primary common cloacal canals and superficial layer of test with embedded pigment are distinctive. The larva, with its long tail wound almost completely around the trunk, is characteristic.

Size and form of the spicules and the large zooids themselves (including the 10 or 11 stigmata in the anterior rows) resemble *D. caesium*. In the latter species spicules are sparse in most of the test, being crowded only in a layer near the surface and one in the basal test, the ray length/spicule diameter ratio is less, an atrial tongue is present, and larvae have more numerous lateral ampullae than the present species. *D. elongatum* and *D. guttatum* have similar large regularly stellate spicules but differ in having unusually long tubular branchial siphons and thick, firm upper layers of test. Some rounded spicule rays and a posterior cloacal cavity also distinguish *D. elongatum*; *D. guttatum* is also distinguished by its relatively few stigmata and numerous larval epidermal ampullae. *D. multispirale* has large spicules (to 0.1mm diameter) but they have more numerous and shorter rays, are more varied and include globular ones, and it has more numerous coils of the vas deferens. *D. stragulum* has similar large stellate spicules and colonies with zooids arranged along each side of primary common cloacal canals. However, the spicules are even larger with slightly fewer rays. Also, it can be distinguished by its pointed surface papillae and ribbon-like pigment cells.

Syntypes of *D. makropnous* (with the exception of ZMA TU461.2 and TU461.6) have similar colonies and spicules to the newly recorded specimens of *D. grande*. The zooids were difficult to remove from the colonies however, and although they are a similar size to the newly recorded specimens, with up to 10 stigmata per row, the retractor muscles were not detected. The small spicule-filled pointed papillae associated with each branchial aperture on the surface of ZMA TU461.6 have the large spicules and circular cloacal canals surrounding opaque zooid-free pillars of test characteristic of *D. stragulum* and ZMA TU461.2 is *D. perplexum*.

The holotype of *D. grande* from the Philippines is described as a large encrusting colony to 8cm, with its surface produced into some lobes and ridges. This has not been located, although a slide of 3 vertical sections of the

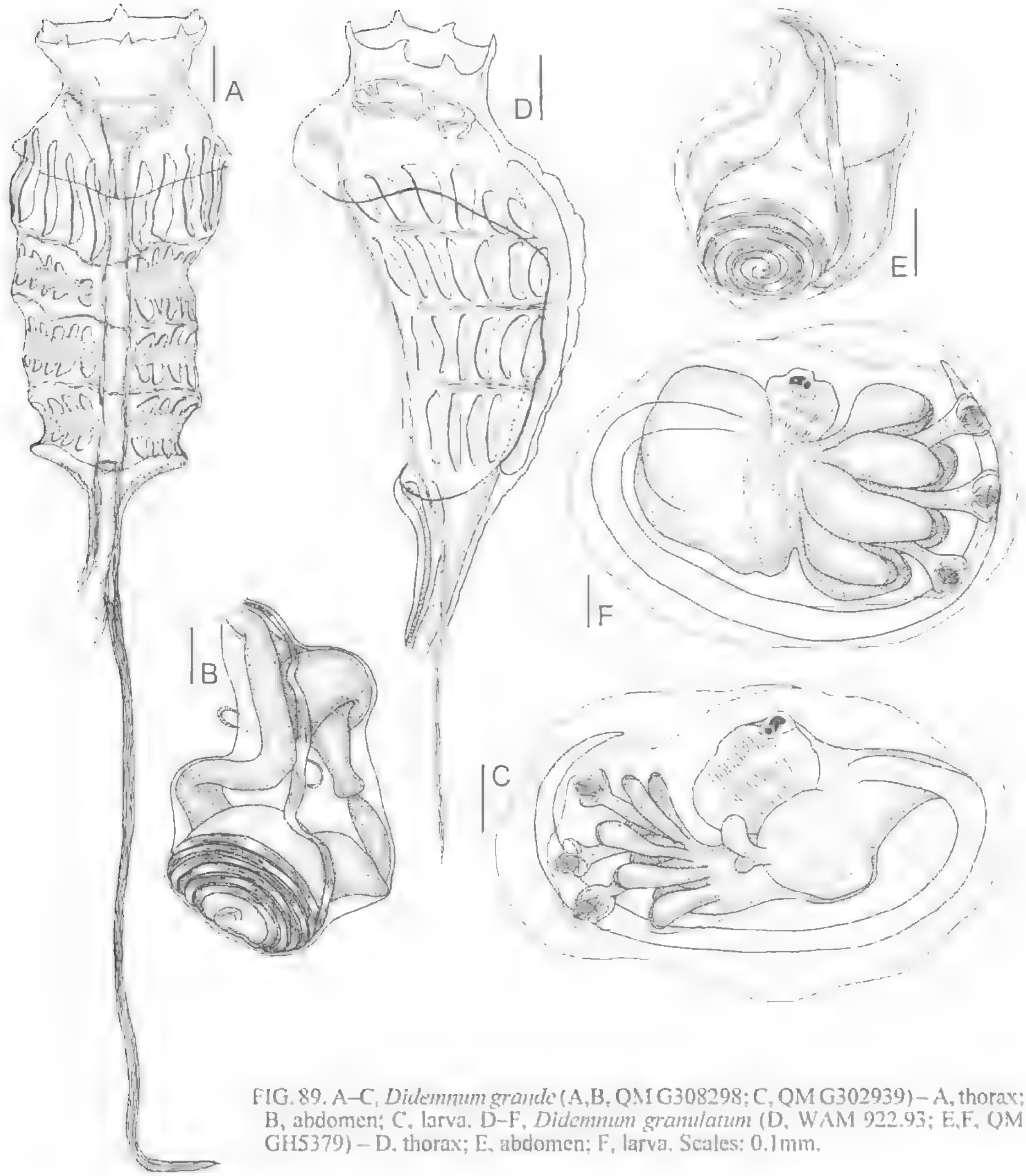


FIG. 89. A–C, *Didemnum grande* (A,B, QM G308298; C, QM G302939) – A, thorax; B, abdomen; C, larva. D–F, *Didemnum granulatum* (D, WAM 922.93; E,F, QM GH5379) – D, thorax; E, abdomen; F, larva. Scales: 0.1mm.

colony, one decalcified, has been examined. The stellate spicules to 0.07mm in diameter, and with 9–11 sturdy pointed rays are crowded throughout. Robust zooids are arranged along deep primary common cloacal canals to form the reticulum that Herdman reported. Zooids are in clumps between these canals and secondary common cloacal spaces penetrate amongst them at thorax level. The vas deferens has 7 coils around an undivided testis. The spicules, colony and zooids resemble the syntypes of *D. makropnous* Sluiter, 1909, of which it is the senior synonym.

Few of the Philippine specimens Van Name (1918) assigned to this species have the characteristic spicule rays and most appear to have been wrongly assigned (Millar, 1975). Kott

(1962) also erroneously assigned a specimen from Rottnest I. with what was thought to be a 2 lobed testis to the present species, largely on the basis of its crowded spicules. However, there is no indication from Herdman's description that *D. grande* (Herdman, 1886) has a divided testis and although Millar (1975) implied that 2 testis follicles (as in *D. recurvatum*) were reported for *D. grande*: Van Name, 1918, this is not so and these are all separate species (see Remarks, *D. bisectatum*, *Polysyncraton oceanium* and *P. palliolum*).

Didemnum granulatum Tokioka, 1954
(Figs 89D–F, 171F; Pl. 9E,F)

Didemnum (Didemnum) moseleyi f. granulatum Tokioka, 1954: 244; 1967: 67.
Didemnum moseleyi: Eldredge, 1967: 210 (part).
Didemnum granulatum: Kott, 1981: 167. Monniot & Monniot, 1987: 31
Didemnum pele: Eldredge, 1967: 197.

NEW RECORDS. Western Australia (Montebello Is WAM 922.93; Cervantes, WAM 176.87). Queensland (Whitsunday Is, QM GH5379; Hardy Reef, QM G300923; Bowden Reef, QM G302892). Northern Territory (Bathurst I., QM GH5748).

PREVIOUSLY RECORDED. Tokara Is (Tokioka, 1954). Fiji (Kott, 1981). Palau Is (Tokioka, 1967). French Polynesia (Monniot & Monniot, 1987). Hawaii (Eldredge, 1967).

COLONY. Colonies are hard but thin and flexible sheets. Spicules are present throughout, sometimes, but not always, so crowded that the test is hard and brittle.

Usually the common cloacal cavity is a large horizontal space crossed by test connectives containing zooids, sometimes in clumps of 2 or 3. The surface layer of test is thin containing only one layer of spicules, and in living colonies is seen to be inflated. One colony (QM G302892) has only a shallow horizontal cavity at thoracic level and abdomina embedded in the basal layer of test. Otherwise only larvae are embedded in the basal layer of test. Occasionally (WAM 176.87) small spicule-filled papillae protrude from the surface of the colony. Two specimens (WAM 922.93, QM G302892) have large vesicles embedded in the test making the surface appear foamy. The stellate branchial apertures are lined with spicules. Common cloacal apertures, randomly distributed on the surface, are circular and protrude slightly in the living colonies.

Spicules are small (to 0.06mm diameter) and have 7–9 and occasionally 5 conical rays in optical transverse section. The rays are relatively long, the ray length/spicule diameter ratio about 0.375. Living colonies are light pink (QM GH5379) or cream, orange-red (QM G302892); or vermilion[R], poppy red[R], geranium red[R], cadmium orange[R], vinaceous buff[R] or salmon colour[R] (Kott, 1981).

ZOOIDS. Zooids are small, the branchial siphon short, with small branchial lobes. The atrial aperture is a wide sessile opening without an atrial lip. About 6 stigmata are in the anterior row, but only 4 short, oval stigmata are in the last row. A retractor muscle projects from about halfway down the oesophageal neck. The testis is almost spherical, against the dorsal part of the ventrally flexed post-pyloric part of the gut loop. Six coils of the vas deferens surround the testis.

Larvae in the basal test of specimens from the Whitsunday Is and Hardy Reef collected in October (QM GH5379, G300923) and from Fiji in July (Kott, 1981) have a trunk 0.7mm long. Those in a colony from Bowden Reef (QM G302892) collected in February, have a trunk 0.35mm long, but are not well advanced. Larvae from French Polynesia (Monniot & Monniot, 1987) and the Tokhara Is (Tokioka, 1954) have larval trunks 0.4mm, 0.3mm long, respectively. They have 4 epidermal ampullae on each side of the 3 antero-median adhesive organs.

REMARKS. The species is characterised by its relatively small, simple stellate spicules with long rays, small zooids and larvae, 6 coils of the vas deferens and horizontal common cloacal cavity.

D. granulatum Tokioka, 1954 was described from the Tokara Islands as a sub-species of *D. moseleyi*. However, the view that the spicules resemble those of *D. moseleyi* (see Kott & Goodbody, 1982; Nishikawa, 1990) cannot be sustained. Its characteristic stellate spicules to 0.04mm in diameter have 5–9 conical rays in optical transverse section Occasionally it has spicule filled surface papillae as in other species (e.g. *D. clavum*, *D. cuculliferum*, *D. membranaceum* and *D. perplexum*). In addition to the spicule size, it differs from *D. perplexum* in its smaller (about half the size) and less robust zooids, lack of darkly pigmented zooids, 4 (rather than 6) larval lateral ampullae per side, 6 coils of the vas deferens (rather than 7) and a thin layer of surface test. Although Rocha & Monniot (1993) stated that the species is present with *D. rodriguesi* in both the Pacific and Atlantic Oceans there is no evidence that this is so as the surface papillae which they believed would

distinguish these species occur only sometimes in this and other *Didemnum* spp.

Didemnum guttatum
Monniot &Monniot, 1996
(Figs 90A,B, 168-I; Pl. 9H)

Didemnum guttatum Monniot & Monniot, 1996: 153.

NEW RECORDS. Queensland (Heron I., QM G308097; Swain Reefs, QM G305451; Whitsunday Is, QM G302876; Dingo Reef, QM GH5423).

PREVIOUSLY RECORDED. Indonesia (North Sulawesi – Monniot & Monniot, 1996). Coral Sea (Eastern Fields Atoll – Monniot & Monniot, 1996).

COLONY. Colonies are thin hard encrusting sheets with the zooids opening along each side of deep primary canals (over which the surface test is slightly depressed) that surround oval to elongate slight surface prominences over stands of zooid-free test. The thin surface layer of test depressed over the common cloacal canals is translucent while the prominences they surround, on top of a depth of spicule-filled solid test, are white and opaque. Zooids are madder brown, pale green or white in preservative, and large pools of green cyanophytes are in the basal test. Living colonies were heliotrope purple[K] with dahlia purple[K] zooids. Minute greenish-brown cyanophytes are embedded in the surface layer of test.

Stellate spicules are crowded in the test and are especially packed in the basal layer which has a hard, rippled surface. The rays are truncated or round-tipped or pointed. They are to 0.08mm diameter, with 9–11 rays in optical transverse section, well separated from one another on the central mass of the spicule. The ray length/spicule diameter ratio is about 0.25.

ZOOIDS. Zooids are less than 1mm long, of which the long narrow branchial siphon, the short small thorax, the long oesophageal neck and the gut loop are each about one quarter. Six small points are around the rim of the branchial aperture. The atrial opening is a sessile transverse opening without an atrial tongue and a retractor muscle of variable length projects from the top to halfway down the oesophageal neck. The branchial sac is small with 6 oval stigmata in the anterior row, reducing to about 4 in the last row. Clusters of greenish-brown pigment are in the rounded gut loop. The stomach is relatively small. Mature testes, each surrounded by 8 coils of the vas deferens are in QM G302876.

Developing embryos are in the newly recorded colony from Dingo Reef, collected in November. Larvae have a trunk to 1mm long and a wide circle of about 24 short, rounded ectodermal ampullae around the antero-median adhesive organs. The adult organs are not well formed (the pharynx is not perforated and the gut is not formed) and 4 characteristic masses of green cells are in the larval test dorsal and ventral to the tail insertion, anterior to the oozooid and tucked into the waist of the larval trunk on the ventral surface.

REMARKS. The species is distinguished by its small thoraces, and long and narrow branchial siphons, stellate spicules with sturdy pointed conical rays as well as spicules with round-tipped or truncated rays, numerous ectodermal ampullae and large larval trunk.

Although symbiotic algae were detected in the surface test of the newly recorded colonies, Monniot & Monniot (1996) did not detect them in the Coral Sea material. The 4 clumps of green cells in the larval test are identical in all known larvae of this species. The species does resemble *D. viride*, which also has green cell symbionts, and the colonies and their colour resemble the present species. *D. guttatum* is distinguished from *D. viride* by its long branchial siphons, more numerous coils of the vas deferens and more ectodermal ampullae, fewer stigmata, and more numerous and shorter spicule rays.

D. poecilomorpha has a similar long branchial siphon and oesophageal neck, and a mixture of stellate spicules, some with relatively short conical rays and others with round-tipped rays. The present species has slightly smaller zooids, more larval ectodermal ampullae and fewer spicule rays. *D. elongatum* Sluiter, 1909 has an equally long branchial siphon but more and longer spicule rays as well as blunt tipped ones. Larvae and spicules of this species resemble those of *D. caesium* but in the latter species spicules are absent from the middle layer of the colony and 10 stigmata are in the anterior rows rather than the 6 recorded for the present species. *D. grande* also has similar spicules but is distinguished by aspects of its colony, more stigmata and only 4 pairs of larval ampullae. *D. ossium* has similar larvae and long branchial siphons but smaller spicules with more and longer rays and a 3-dimensional cloacal system.

Didemnum herba sp. nov.
(Figs 90C, 172D; Pl. 10A)

TYPE LOCATION. Queensland (Wedge Big Broadhurst Reef between Little-Big Broadhurst 11m., coll AIMS Bioactivity Group 01.2.87, holotype QM G308641).

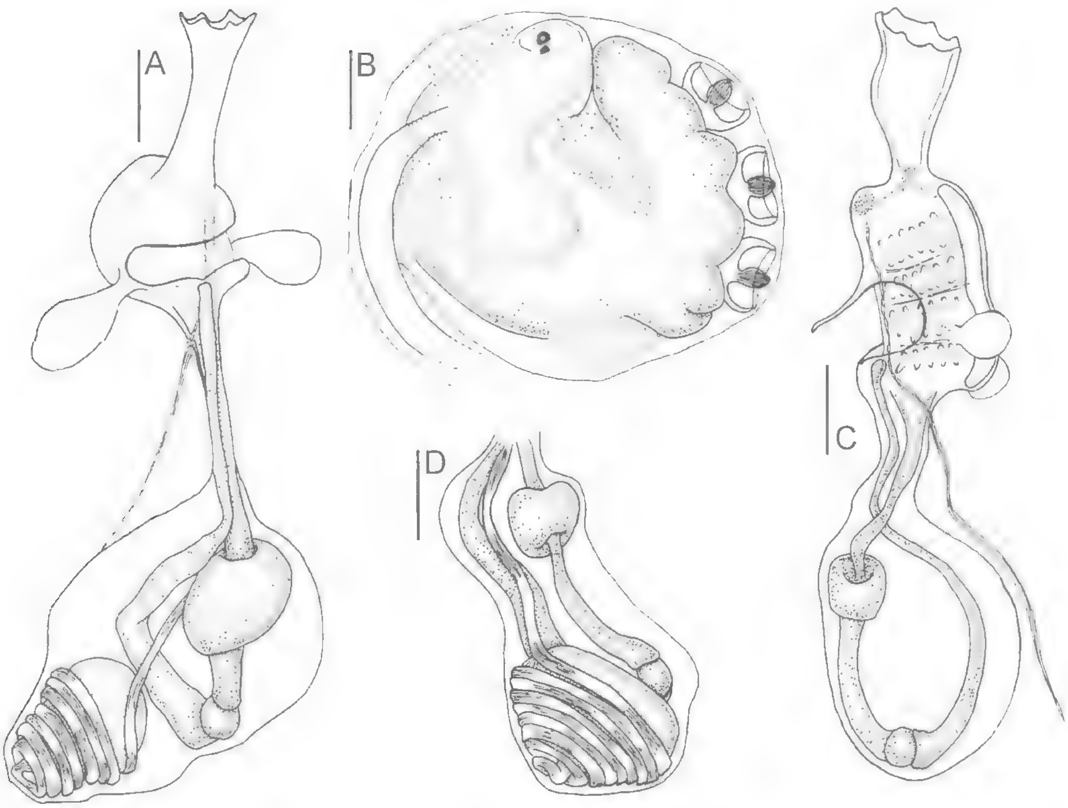


FIG. 90. A, B, *Didemnum guttatum* (A, QM G302876; B, QM GH5423) – A, zooid showing lateral organs projecting from contracted thorax and long branchial siphon; B, immature larva showing characteristic clumps of green pigment. C, D, *Didemnum herba* (QM G308641) – C, zooid; D, abdomen. Scales: A,C,D, 0.1mm; B, 0.2mm.

COLONY. The colony is a thin, hard sheet, white with a pale greenish tinge in preservative. The preservative is stained a pale green. In life the colony is plum-coloured. Oval masses presumably of chlorophytes are in the basal test and spicules are crowded throughout. The cloacal cavity is shallow, at thorax level.

Spicules are stellate to 0.07mm diameter, with 7–9 spiky pointed rays with their bases well separated from one another on the central mass. Ray length/spicule diameter ratio is about 0.25.

ZOOIDS. Zooids, small and well spaced, are about 0.8mm long, and the thorax (including the branchial siphon) and the abdomen (including the oesophageal neck), are about equal lengths. The long branchial siphon, from half to the same length as the remainder of the thorax, is funnel shaped, and has 6 small points around its rim. A small atrial lip is present on the anterior rim of the opening. The branchial sac has 6 stigmata in the first of the 4 rows. A small trumpet-shaped lateral organ projects from each side of the thorax opposite the last row of stigmata, with its concavity directed ventrally. A fine, tapering retractor muscle separates from about one-third of the distance down the oesophageal neck. The gut makes an open loop, with the ascending limb kinked up over the testis, which is undivided and has 8 coils of the vas deferens around it.

REMARKS. Although colony colour and form, spicule size and ray number and contained symbionts resemble *D. guttatum*, *D. poecilomorpha*, *D. verdantum* and *D. viride*, the present species is distinguished by its spiky and relatively short spicule rays, smaller zooids and long branchial siphons.

The oval masses of symbionts in the basal test are found in most other large sheet like species containing possible chlorophyte symbionts embedded in the test, viz. *D. poecilomorpha* and *D. guttatum* (which are distinguished by their more numerous spicule rays and diverse

spicules) and *D. viride* (with stellate spicules but less spiky spicule rays than the present species). *Prochloron*-containing didemnids have either globular spicules (*D. molle*, *D. flavoviride*) or fewer and longer rod-like (*D. verdantum*) or long conical rays (*D. etiolum*). *D. molle*, *D. flavoviride* and *D. etiolum* are further distinguished by their colony forms. The spicules most resemble those of *D. roberti*, which also have long, attenuated, spiky rays.

Didemnum hiopaa Monniot & Monniot, 1987
(Figs 91A,B, 166D)

Didemnum hiopaa Monniot & Monniot, 1987: 32. Monniot, 1995: 311.

NEW RECORDS. Queensland (Heron I., QM G308118, G308308).

PREVIOUSLY RECORDED. West Pacific (New Caledonia – Monniot, 1995; French Polynesia – Monniot & Monniot, 1987)

COLONY. Colonies are small flat plates, less than 5mm diameter, with a central common cloacal aperture and zooids around the periphery of the colony, forming a single system. They often are found on *Halimeda*. In life they are fluffy looking, transparent or translucent and some (QM G308308) are magenta[R] coloured. Large black spherical pigment cells crowd the surface test of the magenta[R]-coloured colonies. Some pink colour sometimes is present in parts of these colonies. Patches of small spicules are between and around the zooids and are scattered sparsely through the remainder of the test. Spicules are absent completely only from the superficial bladder cell layer (which is thicker around the margin of the colony. The common cloacal cavity is shallow, at thorax level, and the surface test is thin. One or 2 common cloacal apertures are in the centre of the upper surface and spicules are absent from their rims. The spicules are small (to 0.028mm diameter) and globular with many rod-like rays.

ZOOIDS. Zooids are small, to about 1mm long. The abdomen is longer than the thorax. The branchial siphon is a wide, short cylinder, about one-third of the length of the thorax, with 6 short sharp points around the aperture. The retractor muscle is short and stout, arising from halfway down the oesophagus. Eight stigmata are in the first 2 rows in the branchial sac; and 7 and 6 respectively are in the other rows.

The distal end of the robust gut loop is flexed ventrally, and a large dome-shaped testis is against its postero-dorsal surface. The vas deferens makes 9 crowded turns around it.

Larvae are not in the newly recorded colonies, but identical larvae were present in the French Polynesian and New Caledonian specimens. They are reported to have a trunk 0.5mm long with 4 ectodermal ampullae, each side of 3 antero-median adhesive organs, a tail wound halfway around the trunk and a vertical oozooid in the middle of the trunk (Monniot & Monniot, 1987; Monniot, 1995).

REMARKS. Spicules of this species resemble *D. albopunctatum*, which differs in its large encrusting sheet-like colonies, small branchial siphons, crowded spicules, the consistency and colour of the colonies, and only 2 larval adhesive organs.

Didemnum incanum (Herdman, 1899)
(Figs 91C-F, 170C; Pl.10C,D)

Leptoclinum incanum Herdman, 1899: 90.
Didemnum moseleyi: Kott, 1972a: 19 (part, specimens from Carickalinga Head).

NEW RECORDS. South Australia (Edithburgh Jetty, QM G302766; Carickalinga Head, SAM E2850). Victoria (Lorne, AM Z5134, Y2322; Gabo I., SAM E2851, AM Y2289). New South Wales (Illawarra, QM G304555, G304557; The Gap, Sydney Heads, QM 304515)

PREVIOUSLY RECORDED. New South Wales (Port Jackson, syntypes not located).

Recorded depths to 15m (on Shell Harbour Reef off Illawarra).

COLONY. Colonies are small, invariably thin, irregular, encrusting sheets on weed and rubble substrates. In preservative they are opaque and white with small spicules crowded throughout. The upper surface is even and sometimes is smooth, although occasionally minute, flat-topped, spicule-filled papillae project between the markedly stellate branchial apertures. Each branchial aperture has a single marginal row of spicules outlining the opening. Common cloacal apertures may be raised on surface swellings created by thickening of the basal test. A specimen from Victoria (AM Y2322) has unusual surface ornamentation, consisting of a fringe of fine spicule-filled radially arranged filaments framing the anterior end of each zooid, the filaments directed away from the aperture. On some parts of this colony, these short filaments fuse with those from adjacent circles and with the surface test, forming a sponge-like scaffolding or superstructure on the surface. Common cloacal apertures are large, sessile, and surrounded by similar filaments or papillae. The common cloacal cavity is large and spacious at thorax level, each thorax crossing it in

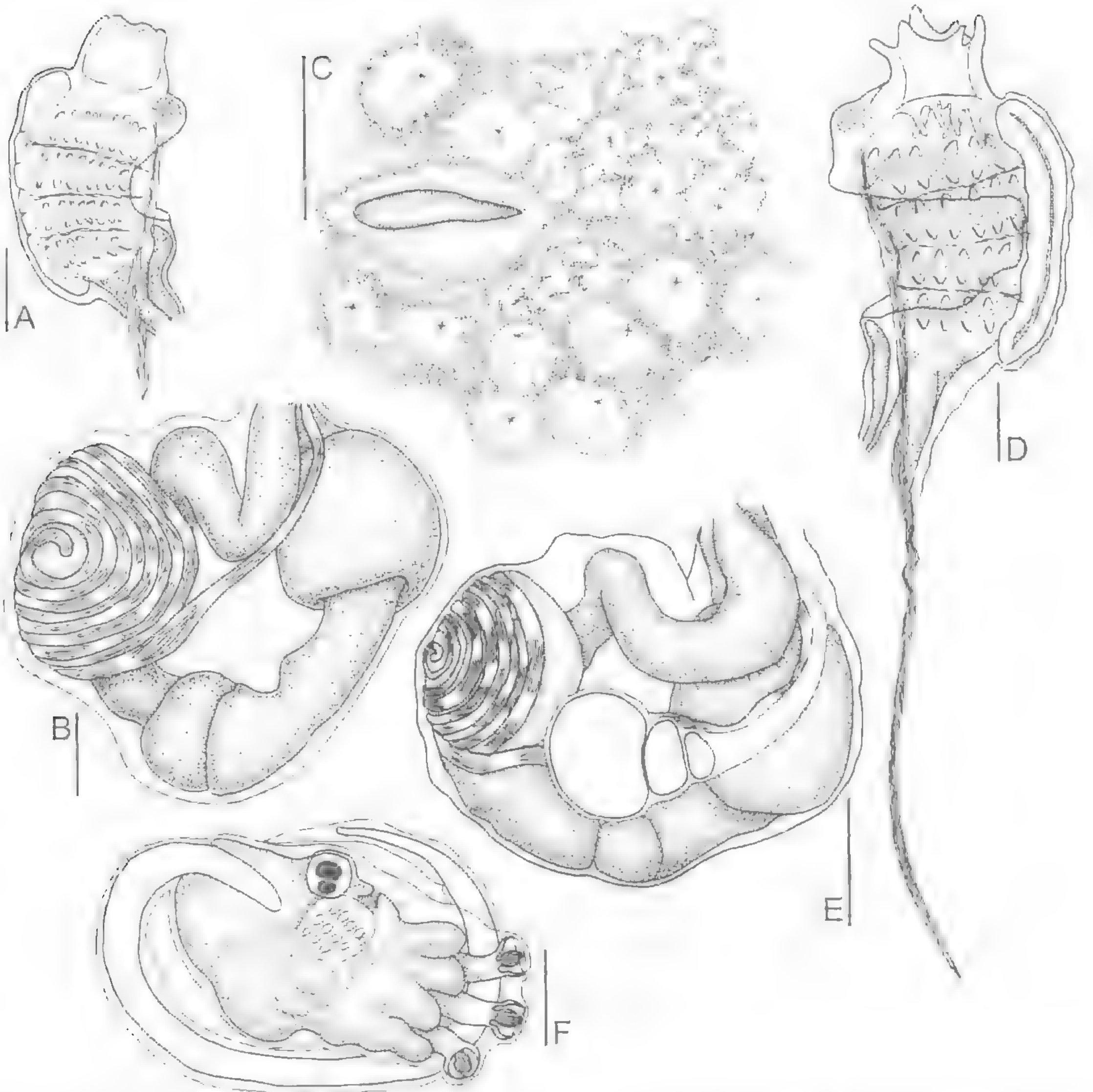


FIG. 91. A, B, *Didemnum hiopaa* (QM G308308) – A, thorax; B, abdomen with gut loop and testis. C–E, *Didemnum incanum* (C,D, AM Z5134; E,F, AM Y2289) – C, colony surface showing pointed papillae encircling some branchial apertures and a large protuberant, elliptical common cloacal aperture; D, thorax; E, abdomen with gut loop and gonads; F, larva. Scales: A,B,D–F, 0.1mm; C, 1.0mm.

an independent test sheath. Spicules are small, always less than 0.04mm in diameter with 5 – 7, and occasionally 9 conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.35.

ZOOIDS. Zooids are narrow and delicate, and even with the thorax extended are less than 1.0mm long. The thorax and abdomen are separated from one another by a relatively short oesophageal neck. The branchial siphon is of moderate length, with 6 sharp points around the rim of the aperture. The paired dorsal pharyngeal muscles have only few fibres, but the retractor muscle in the newly recorded specimens is long and finely tapering and projects from about halfway down the oesophageal neck. The lateral organ is a shallow concavity each side of the atrial aperture and the test plugs from these organs can be seen on each side of the ventral thoracic sheath of the test. The branchial sac is

narrow, with 6 stigmata in each of the first 2 rows and 4 in the last. The posterior pyloric part of the gut loop is sometimes bent up ventrally against the proximal part, although in other specimens it is only slightly ventrally flexed.

A large hemispherical male follicle with 9 tight coils of the vas deferens around its outer half is against the dorsal aspect of the distal part of the gut loop at the posterior end of the zooid. The mature testis is best developed in QM G302766, and AM Z5134, Y2289. Tailed larvae are in specimens collected from South Australia in September (QM G302766), the Illawarra in May (QM G304557) and Gabo I. in February (AM Y2289). The ovary is conspicuous in the last specimen, while the testis is best developed in the first. The species may be protogynous. The larval trunk is about 0.4mm long with the tail wound almost completely around it, an ocellus and otolith, 4 rows of stigmata, and 4 cylindrical ectodermal ampullae along each side of the 3 antero-median adhesive organs. In the specimens from Illawarra the stigmata have not perforated and the ampullae are not yet developed.

REMARKS. The newly recorded specimens have the same small, crowded, stellate spicules and thin, white, opaque colonies as the type material. The long atrial tongue reported by Herdman (1899) has not been detected, and is not a usual character in such small zooids with such delicate musculature. It is not known what Herdman may have been referring to — there is no atrial tongue in his figures.

South Australian *D. delectum* resembles the present species in its small, stellate, crowded spicules with 7–9 rays in optical transverse section, small zooids, spicule-filled surface papillae, a similar number of stigmata and vas deferens coils and a small larva. The present species has 5 stigmata per row (*D. delectum* has 6) and 9 coils of the vas deferens (*D. delectum* has 6) and its spicules are slightly smaller with broader, more conical and relatively short rays. *D. vulgare* has a similar colony but larger spicules. *D. cygnuus* also has small stellate spicules, but they are not crowded throughout and they are less regularly stellate.

Didemnum inveteratum sp. nov.
(Figs 92, 168E; Pl. 10B)

TYPE LOCALITY. Western Australia (Lord Mayor Shoal, 16°31.2'S 122°36.4'E, 21m, coll. AIMS Bioactivity Group 13.8.91, holotype QM G 302922).

COLONY. The holotype colony forms large flat, slightly curved, fan-shaped, double-sided lamella. The colony is hard and rigid. Zooids open all around the outer surface, but are not crowded. Common cloacal canals are shallow and thoracic, with the zooids embedded in test along each side, the atrial apertures opening directly into them. A short narrow atrial tongue projects across the top of the common cloacal canals. The bases of each side of the colony are opposed to one another with a space between them which contains some wisps of what appears to be weed, possibly kelp, which may have been overgrown.

Spicules are crowded in the test at all levels, especially in the basal third of the colony. They are so crowded that there is little test between, to bind them together, and when the test is broken it disintegrates and spicules are released like grains of sand. Spicules are large, to 0.11mm diameter with 13–15 relatively short, usually conical but sometimes blunt or truncated rays. The ray length/spicule diameter ratio of the stellate spicules is about 0.3 and some of the conical rays are sometimes smaller than others.

ZOOIDS. Zooids are small, about 1mm long. The branchial siphon is about half the length of the small branchial sac, which has 6 oval to long rectangular stigmata in the first 2 rows and 5 in the last 2 rows. A small, atrial tongue projects from the anterior rim of the large sessile aperture. A tapering retractor muscle projects from the posterior end of the zooid at the top of the oesophageal neck. The oesophageal neck is relatively long and the gut forms a fairly open loop. Only spent testes are in the holotype, and in some of the zooids, remnants of about 5 coils of the vas deferens are present, distended with sperm.

REMARKS. The species is characterised by its small zooids with small atrial lip, hard colonies with shallow common cloacal spaces and large spicules crowded throughout the test, especially in the base of the colony.

D. apuroto, *D. bicolor*, *D. diffundum* and *D. ossium* also have pointed, truncated spicule rays, but they do not exceed 0.07mm diameter, and their cloacal systems and colonies are different from the flat sheets of the present species. *D. stragulum* has similar sized spicules but with longer and fewer rays, the spicules are not as crowded and their rays are not truncated. *D. toafene* Monniot & Monniot, 1987 has similar thin, hard colonies. However, although its zooids

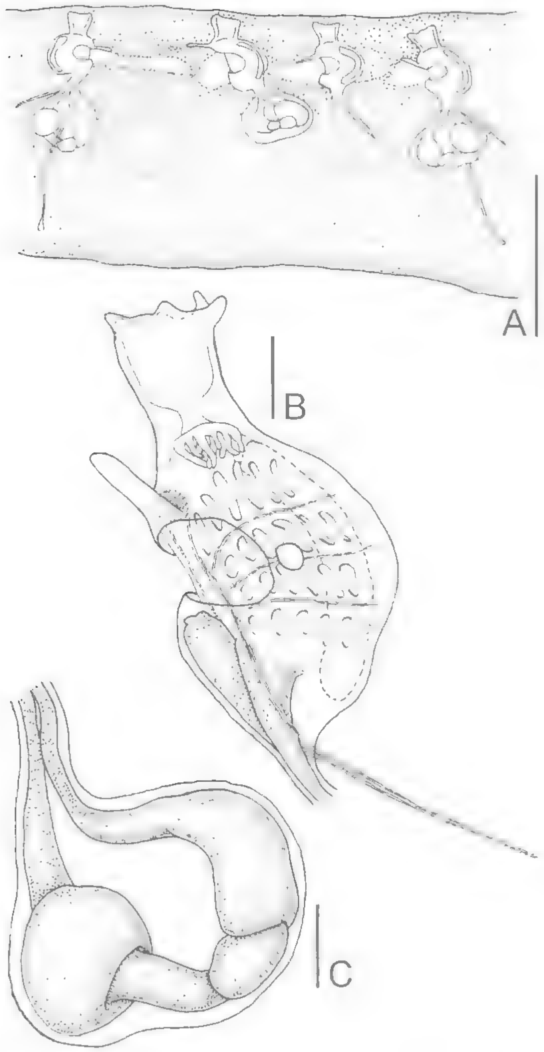


FIG. 92. *Didemnum inveteratum* sp. nov. (QM G302922) – A, semidiagrammatic vertical section through colony; B, thorax; C, gut loop. Scales. A, 1.0mm; B,C, 0.1mm.

are small they lack an atrial tongue and they have 10 coils of the vas deferens (which seems more than the number likely to occur in the present species), and neither the small spicules with fewer rays nor the larger ones with longer rays have the truncated rays of the present species. The temperate *D. microthoracium* has large (to 0.09 mm diameter) spicules embedded throughout, and thoracic common cloacal canals. However, it has more regularly stellate spicules than the present species.

Didemnum jedanense Sluiter, 1909
(Figs 93, 167G; Pl. 10E,F)

Didemnum jedanense Sluiter, 1909: 59 (part, ZMA TU454.1 statn 89). Hastings, 1931: 99 (part, specimen from statn XII).
Didemnum reticulatum Sluiter, 1909: 60 (part, ZMA TU475.4, TU475.5).
Not *Leptoclinides reticulatus*: Hastings, 1931: 32 (< *L. rufus*). Monniot & Monniot, 1996: 178.
Didemnum albopunctatum Sluiter, 1909: 58 (part – ZMA TU433.3 part, specimens with narrow rod-like spicule rays; ZMA TU433.4).
Didemnum cineraceum: Monniot, 1995: 303.
Didemnum pseudodiplosoma ? : Monniot, 1995: 324.

NEW RECORDS. Western Australia (Cape Ruthiers, QM G300976). Queensland (Hervey Bay, QM G9274, G308449, G308491; Heron I., QM G301556, G302567 G302963, G308294; Abbot Point, QM G300927; Mossman, QM G302160; Lizard I., QM G301533, G302028).

PREVIOUSLY RECORDED. Queensland (Low Is – BMNH 30.12.17.63, 30.12.17.66 Hastings 1931). Indonesia (ZMA TU475.4, TU475.5, TU454.1, TU433.3 part, TU433.4 Sluiter, 1909). New Caledonia (Monniot, 1995).

COLONY. Colonies are large (to 10cm maximum dimension) gelatinous sheets with irregular rounded margins, about 3mm thick. The surface is divided into flat polygonal sections by a network of depressions over the deep common cloacal canals that surround each clump of zooids. These depression are emphasised by the dark, oval or spherical to comma-shaped granular pigment cells, about 0.015–0.025mm diameter, that are most crowded around the zooid openings along each side of the cloacal canals, and over the top of the canals themselves as well as around the outer margin of the colony. These granular cells are in the surface bladder cell layer of test.

Although some colonies (QM G301556, G302028) are aspicular, others have clouds of minute white spicules beneath the bladder cell layer. Sometimes spicules are confined to the test over the zooids; or they are between the zooids continuing into a layer in the base of the common cloacal cavity, being absent from the test over the common cloacal canals and the base of the colony. Spicules are burr-like, small (up to 0.04mm diameter) with up to 19 long, rod-like, striated rays in optical transverse section. The tips sometimes are rounded, seldom pointed, and sometimes very irregular and frayed. The ray-length/spicule diameter ratio is about 0.4.

In life one colony from Lizard I. (QM G301533) contained pansy purple[R] pigment particles, and another (QM G302028) had heliotrope purple[R] zooids with translucent test. A

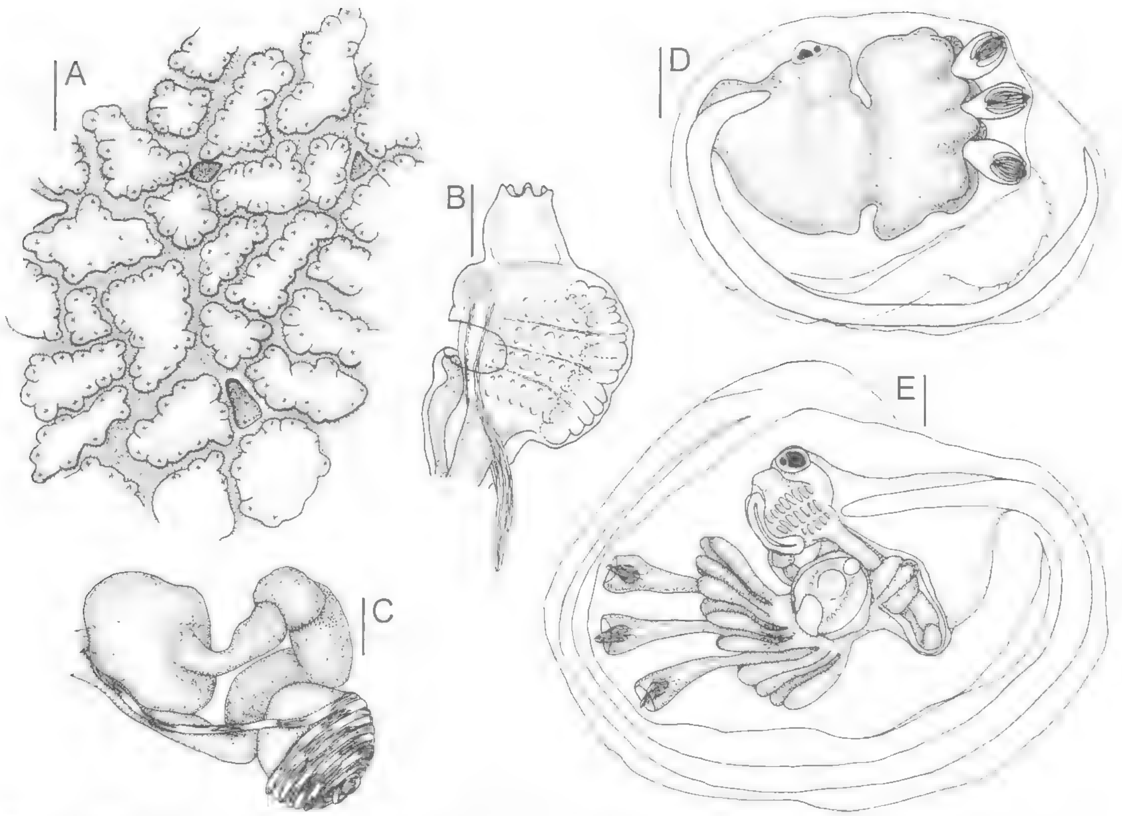


FIG. 93. *Didemnum jedanense* (A,B, QM G308449; C, QM G308294; D, QM G302160; E, QM G301533) – A, surface of colony; B, thorax; C, gut loop and testis; D, early larva; E, mature larva with thoracic and abdominal buds on left and right of trunk respectively. Scales: A, 2.0mm; B–E, 0.1mm.

colony from Heron I. had a transparent test with yellow zooids, one from Abbot Point is reported to have been black and white and one from Cape Ruthiers was white and grey. Dark granular cells in the superficial layer of test over the common cloacal canals and around the margins of the colony persist in preservative but eventually are lost and the test becomes translucent with cream to beige zooids. Variations in colony appearance in life result largely from concentrations of spicules.

ZOOIDS. Zooids are robust and relatively large, being about 2mm long, although the contracted thorax (including a long cylindrical siphon which is 0.2mm long) is only about 0.5mm long. The oesophageal neck is about one-third of the length of the zooid and a short to long, finely tapering retractor muscle projects free from about halfway down it. The 6 branchial lobes around the rim of the aperture are deep and rounded. The sessile atrial aperture exposes the middle of the dorsal half of the branchial sac directly to the common cloacal cavity. About 10 stigmata are in the anterior row of the branchial sac, although the exact number could not be determined as all the thoraces examined are very contracted. The gut loop is rounded. Eight coils of the vas deferens surround an undivided testis. A lateral organ is about halfway down each side of the thorax, near the rim of the atrial aperture.

Larvae are in colonies from Lizard I. taken in June (QM G301533, G302028), NW Australia in August (QM G300976), Heron I. in November (QM G301556), Mossman in February (QM G302160), Abbot Point in March (QM G300927) and Hervey Bay (QM G308491). Embryos at all stages of development are in the basal test and mature larvae are in the surface test and probably are released through the surface of the colony. The trunk is oval to almost spherical and 0.7–1.2mm long. The tail is wound barely halfway around it. Larvae from Mossman and Hervey Bay are at an early stage of development, having 4 or 8 short ectodermal ampullae per side

on a large frontal plate separated from the oozooid by a deep constriction. The larger and better developed larvae from other locations have 8 long, slender ampullae on each side of the 3 median adhesive organs. In the centre of the trunk is an oozooid and one blastozooid (an abdominal bud on the right and a thoracic bud on the left of the thorax). The oozooid has 3 rows of stigmata and the blastozooid 4. The adhesive array is constricted off from the rest of the embryo by a narrow neck leaving the oozooid and blastozooid, respectively, projecting dorsally and laterally. Posteriorly the larval trunk tapers to a narrow cone around the base of the tail. In larvae from Abbot Point (QM G300927) either the dorsal or the ventral adhesive organs tend to fuse with the central one, resulting in 2 adhesive organs.

REMARKS. The soft, gelatinous colony, with sparse, small, burr-like spicules absent from the surface and basal layers and often from the test over the common cloacal canals resembles *Diplosoma*, although the zooids are more contractile than is usual in that genus. The soft colonies, small spicules and their distribution, and the network of black spherical cells in the superficial layer of test distinguish the species from other *Didemnum* spp. The larval trunk, narrowing posteriorly with a narrow waist behind the adhesive array, 8 long and narrow ectodermal ampullae per side and the oozooid thorax and blastozooid projecting out from the trunk resemble some *Polynsyncraton* and *Lissoclinum* larvae and are unusual in *Didemnum*

Hastings' (1931) re-examination of type specimens indicated that Sluiter's description of *D. jedanense* probably was based on the specimen from Siboga Station 89 (ZMA TU454.1) which has small (0.025mm diameter) spicules with numerous rays. Specimens from Siboga Stations 273 and 303 (ZMA TU454.2, TU454.3) were found to be different species, with spicules crowded throughout (see *D. perplexum* and *D. multispirale*, respectively). Hastings also reported a surface layer of bladder cells and spindle-shaped pigment cells in *D. jedanense*, and confirms Sluiter's report of bladder cells in the basal layer of test where spicules are in reduced concentrations.

Although Hastings (1931) thought that the Low Is specimens had spicules smaller than those of Sluiters' (1909) *D. jedanense*, the spicules of *D. jedanense*: Hastings, 1931 (BMNH 30.12.17.63, statn XIX 30.12.17.66) are found on re-examination to be much the same size as those of the lectotype of *D. jedanense* Sluiter, 1909 (ZMA TU454.1) and they closely resemble the spicules of the newly recorded specimens. The Low Is specimens also contain dark granular, oval cells like those of the newly recorded specimens.

Sluiter (1909) distinguished *D. jedanense* from *D. reticulatum* by its slightly larger spicules, of about 0.025mm diameter or more. This difference has not been confirmed by the present study in which spicules of a similar size have been found in syntypes of *D. reticulatum*.

A similar distribution of bladder cells and spicules as those found in *D. jedanense* is reported for *D. reticulatum*. *D. reticulatum* Sluiter, 1909 is a problematic species because of the large number of different taxa initially assigned to it. All these subsequently were designated syntypes (Spoel, 1969). Hastings (1931) had assumed that ZMA TU475.1 (which she found to be a *Leptoclinides* sp.) would be the lectotype. She did not examine the other specimens that Sluiter (1909) had assigned to the species, believing they would be conspecific and that Sluiter had mistakenly assigned the species to *Didemnum*. It now appears that Sluiter may not have examined the zooids of all the colonies he assigned to this species. His (1909) description of *D. reticulatum* is of gelatinous colonies, with crowded bladder cells and blotches of dark colour sometimes forming a network on the surface. The specimens on which he appears to have based the species are ZMA TU475.4 and TU475.5. Re-examination of these specimens shows them to have spicules generally about 0.02mm in diameter but with some to 0.035mm and to have 13–15 long rod-like rays in optical transverse section — generally conforming with the small (to 0.025mm diameter) spicules that Sluiter stated to be characteristic of the species. The other specimens he assigned to *D. reticulatum* have larger and always different spicules from those he recorded for the species and they are *Leptoclinides marmoratus* (ZMA TU475.3); *Leptoclinides rufus* (ZMA TU475.1, TU475.2, TU475.7); *Leptoclinides cuspidatus* (ZMA TU475.9); and 2 specimens of *D. caesium* (ZMA TU475.6, TU475.8). Accordingly ZMA TU475.4 and TU475.5 are here designated as the only syntypes of *D. reticulatum*. They also conform with the lectotype specimen of *D. jedanense*. Thus *D. reticulatum* and *D. jedanense* are conspecific, having similar zooids, cloacal

systems and spicules and similar distribution of spicules and bladder cells.

D. cineraceum: Monniot, 1995 from New Caledonia has encrusting colonies and zooids with a similar number of vas deferens coils and a larval trunk more than 1.0mm long with the same number of larval ampullae (8), a larval blastozooid and spicules of the same size and form as the present species with which it is conspecific. The Atlantic species, *D. cineraceum* (Sluiter, 1898), to which Monniot (1995) had assigned her New Caledonian material is distinguished by its large atrial opening and smaller burr-like spicules with more rays than are reported for *D. jedanense*.

D. pseudodiplosoma ?: Monniot, 1995 is considered to be an aspicular colony of the present species having similar zooids and larvae. Of known spicule-free species that could be confused with the present one, *Trididemnum pseudodiplosoma* (Kott, 1962) from St Vincent Gulf also has an unusually large larval trunk (about 1.2mm long) and at least 8 pairs of lateral ampullae. As well as having 3 rows of stigmata, it differs from the present species in its more numerous larval blastozooids. *D. okudai* Tokioka, 1951, *D. flagellatum* Tokioka, 1953 and *D. pacificum* Tokioka, 1953 from Japan, and *D. elikapekae* Eldredge, 1967 from Hawaii also lack spicules. *D. flagellatum* and *D. elikapekae* have small larvae with only 4 lateral ampullae per side, and they lack a blastozooid. *D. pacificum* has only 4 coils of the vas deferens, and *D. okudai* has sand grains throughout the test.

D. jedanense resembles *D. hiopaa* Monniot & Monniot, 1987 in its spicules, in their absence from some parts of the colony and in the shape of the larval trunk, although *D. hiopaa* lacks larval blastozooids and has only 4 pairs of ectodermal ampullae. *D. jedanense* resembles *D. chartaceum* in the presence of bladder cells in the lower half of the colony where spicules are sparse, but the spicules are different in form, those of *D. jedanense* being smaller than those of *D. chartaceum*, and the zooids of *D. chartaceum* have an atrial lip.

D. arancium, D. chartaceum, D. levitas, D. multispirale and *D. precocinum* also have blastozooids in the larva, and about 8 ectodermal ampullae in the larval trunk, but they all have larger spicules with more rays; and in none of these species does the posterior end of the larva narrow as it does in *D. jedanense*.

D. dealbatum Sluiter, 1909 has similar but larger spicules (to 0.04mm diameter), and lacks the thick superficial bladder cell layer of the present species.

Monniot (1989) referred to a 'type' of *Leptoclinum reticulatum* Sluiter, 1909, from the Senckenberg Museum, Frankfurt. Sluiter (1909) assigned 9 species to *Leptoclinum* (< *Diplosoma*), but not one carries the name referred to by Monniot, so identity of the specimen she examined is in doubt. *D. reticulatum* Sluiter, 1909 types are in the Zoological Museum, Amsterdam (ZMA 475.1 – .7; Spoel 1969) as discussed above and many have been erroneously assigned (Table 2). Monniot & Monniot, 1969 refer to type specimens of *L. reticulatus* which they found had similar characters to newly recorded specimens of *Leptoclinides* sp. from Papua New Guinea.

Didemnum jucundum sp. nov.
(Figs 94, 167D; Pl. 10G,H)

?*Trididemnum spiculatum*: Kott, 1972a: 16.

TYPE LOCALITY. Western Australia (Esperance, tanker jetty piles near shore, 3 to 6m, coll. K.G. Gowlett Holmes 5.1.93, paratype SAM E2693, photo PE 0180). Victoria (Port Phillip Bay, Portsea Pier piles 4-6m, coll. K.L. Gowlett Holmes 25.7.94, holotype SAM E2646.

FURTHER RECORDS. South Australia (? West I., SAM E2852 – Kott, 1972a; Kangaroo I., QM G302897).

COLONY. The colony forms a robust flexible sheet. The surface layer of test, forming the roof of the cloacal cavity, is relatively thin consisting of a superficial layer of bladder cells over a thin layer of spicules which are mixed with brown pigment. The common cloacal cavity is shallow and thoracic, the small thoraces crossing the cavity in separate ventral test sheaths. The spicule layer continues over the anterior end of the zooids and into the siphonal lining, but there is no conspicuous pattern formed by the apertures or the spicules lining them on the surface of the colony. Zooids are confined to the upper half of the colony. Spicules are evenly, but only moderately crowded throughout most of the test, but seem to be less crowded around the thoraces. They are stellate, large (to 0.08mm in diameter), with numerous (13–15) conical pointed rays in optical transverse section. Occasionally spicules with only about 7 rays in optical section also occur. The ray length/spicule diameter ratio is up to 0.3. The living colonies are black and reservoirs of dark pigment are in the base of the preserved colony. A photograph of one specimen (QM G302879) shows some patches of tan.

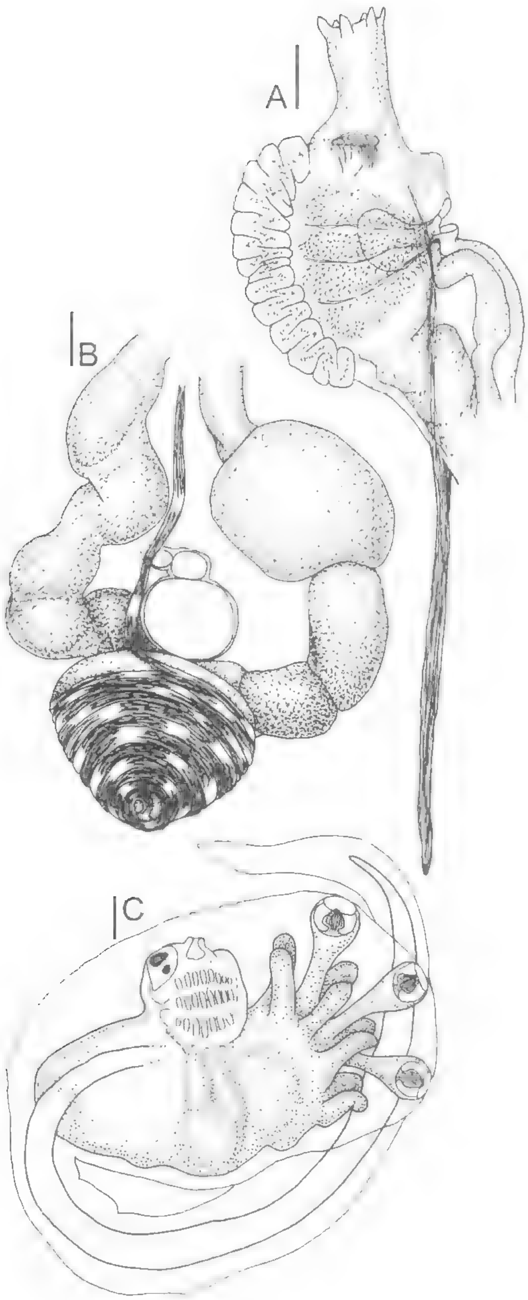


FIG. 94. *Didemnum jucundum* sp. nov. (A,B, SAM E2646; C, SAM E2693) – A, contracted thorax; B, gut loop and gonads; C, larva. Scales. 0.1mm.

ZOOIDS. Zooids are contracted in available specimens, but the following characteristics are apparent. They are large, about 1.5mm long when contracted. Abdomina, embedded in the basal test, are bulky. The branchial siphon is a relatively long and narrow cylinder, with 6 rounded lobes around the rim. The atrial aperture is sessile, exposing a large part of the branchial sac directly to the common cloacal cavity. The oesophageal neck is particularly long, being transversely wrinkled in these contracted zooids. The dorsal pharyngeal bands and some fine bands in the parietal thoracic wall are conspicuous, continuing into the strong, tapering retractor muscle which projects from the oesophageal neck near its base. About 8 stigmata are in the anterior row in the branchial sac, although the exact number is obscured by contraction. Large lateral organs are on each side of the thorax. The abdomen is robust, almost spherical, with the post-pyloric part of the wide open gut loop flexed ventrally to form a distinct double loop. A small ovary is against the flexed part of the gut loop in most zooids in the holotype. In the paratype the vas deferens coils 12 times around the beehive-shaped undivided testis. Occasionally a spent testis, with the vas deferens packed with sperm (acting as a seminal vesicle) is distal to the ovary.

Large larvae are being incubated in the basal test of the paratype. The trunk, about 1mm long and relatively narrow, has the tail wound two-thirds of the way around it. The vertical oozooid is halfway along the trunk, its anterior part projecting up into the larval test. A spherical yolk mass is anterior to the gut loop. Four club-shaped lateral ampullae, with caps of columnar epithelial cells over their tips, are on each side of the long, stout stalks of the 3 antero-median adhesive organs. Three rows of about 8 stigmata, are conspicuous in the larval pharynx. There is no blastozooid.

REMARKS. The species is distinguished by its surface layer of bladder cells, large abdomen with the gut forming a double loop, long oesophagus, long branchial siphons, large hive-shaped testis with particularly numerous coils of the vas deferens, large size range of spicules with numerous and relatively long spicule rays and long larval trunk.

The specimen from West I. (Kott, 1972a) has a similar colony and spicules, although its zooids are immature.

The South Australian *D. delectum* has smaller and more crowded spicules with fewer and longer rays. The sympatric *D. vulgare*, has the retractor muscle from the upper part of the oesophageal neck, a small larval trunk, and smaller spicules without as many rays. *D.*

pellucidum has spicules about the same diameter, but with fewer rays, crowded only in the surface. The sympatric *D. ternerratum* has smaller spicules with more numerous rays packed hard throughout the colony. The spicule distribution and surface bladder cell layer of the present species is slightly reminiscent of the tropical *D. chartaceum* but that species retains its dark pigment in preservative, has virtually no spicules beneath the surface layer, and has a distinct atrial tongue.

Didemnum lacertosum Monniot, 1995
(Figs 95A–B, 167B)

Didemnum lacertosum Monniot, 1995: 311.

NEW RECORDS. Queensland (Wistari Reef, QM G308006; Heron I., QM G302950, G308227; Swain Reefs, QM G308408).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1995).

COLONY. Newly recorded colonies are small delicate plates, to about 1.5mm thick although one (QM G308227) is a thin, white sheet, without pigment and in vegetative phase (without gonads). Living colonies are scarlet vermilion[R] and vermilion[R] to dark (carmine[R]) coloured zooids show through the surface. A conspicuous superficial bladder cell layer contains small scarlet-vermilion pigment cells that also occur amongst the spicules crowded throughout the test beneath the bladder cell layer. Pigment is absent from the test over the branchial apertures, which are white owing to the spicules lining the siphons. In preservative colonies are pinkish-white to white. *Prochloron* is present on the surface. Spicules are up to 0.05mm in diameter, with crowded conical rays, occasionally round-tipped, but mostly pointed, 17–19 in optical transverse section and some are globular with flat-tipped rays.

ZOOIDS. Zooids are small, less than 1mm long when contracted. Although the contracted thorax and abdomen are about the same size, the thorax is probably about twice the length of the abdomen when relaxed. The branchial aperture has 6 small lobes around its rim. The atrial aperture lacks an anterior lip and is wide and open, or contracted into a small transverse opening. The branchial sac has about 6 stigmata in the anterior row, although these could not be accurately counted. About 6 longitudinal muscles in the parietal body wall join the strong dorsal pharyngeal muscles at the posterior end of the body to form the retractor muscle projecting out into the test from the top of the oesophagus. The gut is relatively long, with a long rectum. The posterior pyloric part of the loop is bent ventrally up against the anterior part. Gonads are beneath the flexed part of the gut loop. The dome-shaped testis follicle, with 6 coils of the vas deferens, is distal to a large egg. A pair of bulb-shaped stolonic vessels project from the body wall in the ventral concavity of the flexed gut loop. Larvae, known only for New Caledonian specimens, have a trunk 0.5mm long with 6–8 pairs of lateral ampullae and a single blastozooid (see Monniot, 1995).

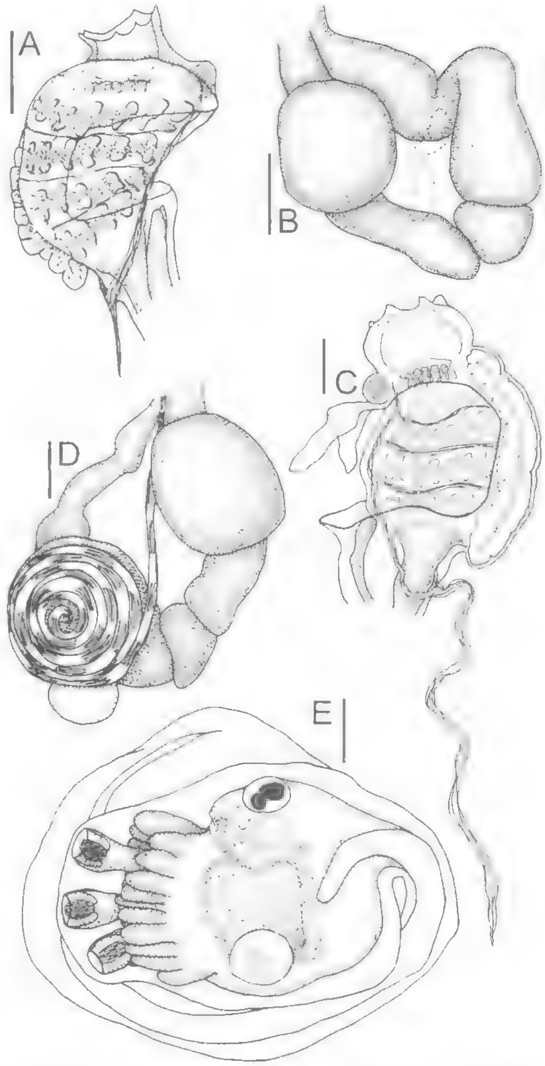


FIG. 95. A–B, *Didemnum lacertosum* sp. nov. (QM G308006) – A, thorax; B, gut loop. C–E, *Didemnum levitas* sp. nov. (C,E, QM G308220; D, QM 308224) – C, thorax; D, gut loop and gonads; E, larva. Scales: 0.1mm.

REMARKS. Spicules resemble those of *D. paa* Monniot & Monniot, 1987, but the latter species has differently arranged systems and more coils of the vas deferens. Zooids and colonies of the thicker orange colonies of *D. ligulum*: Monniot & Monniot, 1987 from French Polynesia (<*D. uranciun*) are similar, but they differ in the bifid atrial tongue and in their spicules with more crowded and conical rays. The spicules have more numerous but shorter conical rays than those of *D. astrum*, also a western Pacific species. Larvae have a blastozooid, as do larvae of *D. uranciun*, *D. chartaceum*, *D. linguiferum* and others, but fewer epidermal ampullae in the larval trunk than the 3 last-named species.

Colonies, zooids and spicules are similar to the type material from New Caledonia. The type material has musculature characteristic of the genus, and despite Monniot's (1995) suggestion, this cannot be a distinguishing character.

Didemnum levitas sp. nov.
(Figs 95C-E, 166H)

TYPE LOCALITY. Queensland (Gorgonia Pools, Heron I. Reef, intertidal, coll. P.Kott et al., 5.9.94, holotype QM G308224, paratype QM G308220).

FURTHER RECORDS. Queensland (Swain Reefs, QM G308439).

COLONY. Colonies are small plates with an even upper surface containing walnut brown[R] or burnt carmine[R] pigment cells, which confer a velvety brick red[R] to dragons-blood red[R] colour to the surface of living colonies. The zooids are saturn red[R]. Large spicules are in a single layer at the surface, making it feel raspy, and a thin layer is just on the base of the colony. Spicules are not present in the centre. They are to 0.06mm diameter, with 17–19 short sharply pointed rays in optical transverse section. Generally the bases of the rays are well-separated from one another on the central spherical mass. Also globular spicules with flat-tipped rays are scattered amongst the stellate ones.

ZOOIDS. Zooids are about 1mm long, with large cup- or turnip-shaped branchial siphons, each with 6 short points around its rim. The branchial sac is large, with 10 long stigmata in the anterior row, reducing to 8 in the posterior row. A robust, wavy retractor muscle projects from near the upper part of the oesophageal neck, a delicate atrial tongue of variable length is on the anterior rim of the sessile opening, but often is torn off when the zooids are removed from the test. It usually is bifid at the tip.

The gut loop is fairly open and circular. It is flexed ventrally. An undivided testis surrounded by 7 coils of the vas deferens lies against the dorsal aspect of, or behind, the flexed part of the gut loop. Eggs are orange. Larvae, in the basal test of the paratype, have a trunk about 0.65mm long, and 10 pairs of ectodermal ampullae along each side of the 3 antero-median adhesive organs. A blastozooid may be present beneath the oozooid (in the middle of the trunk). The tail is wound about three-quarters of the way around the trunk.

REMARKS. Spicules, zooids, and larvae most closely resemble *D. multispirale*. The latter species has more numerous (9) coils of the vas deferens, a characteristically pigmented colony with a yellow and orange (saturn red[R] to flame scarlet[R]) pattern on the surface, zooids opening along each side of the deeper primary common cloacal canals (over which the surface is depressed) and spicules crowded throughout the colony. Also, the larval trunk is longer than in the present species, a long horizontal ampulla on the left side stretches from the waist back to the middle of the trunk and a blastozooid is not present. *D. mutabile* has similar stellate spicules and large branchial siphons to the present species. However, its spicules are crowded throughout the colony, it lacks globular ones, and it has fewer stigmata. *D. lacertosum* lacks the globular spicules and although it has similar stellate spicules, they are crowded throughout and their rays are more crowded, and it has a superficial layer of bladder cells and only 6 coils of the vas deferens.

Didemnum linatum sp. nov.
(Figs 96A, 169F)

TYPE LOCALITY. Western Australia (51 n. miles NNE of Port Hedland 38m, coll. L. Marsh and M. Bezant on FRV Soela 4.10.82, holotype WAM 40.89).

COLONY. The colony is a thin, translucent, sheet with a relatively sparse, but even layer of spicules in the surface test. The common cloacal cavity occupies most of the colony depth, and the basal layer of test is thin. Individual zooids or small clumps of 2 or 3 are supported in thin but short test connectives that join basal to surface layers of test.

Spicules are large (to 0.12mm diameter) and stellate with 9-11 pointed conical rays, in optical transverse section. The ray length/spicule diameter ratio is only about 0.2.

ZOOIDS. The small (less than 1.0mm long) zooids have narrow thoraces with about 6 stigmata

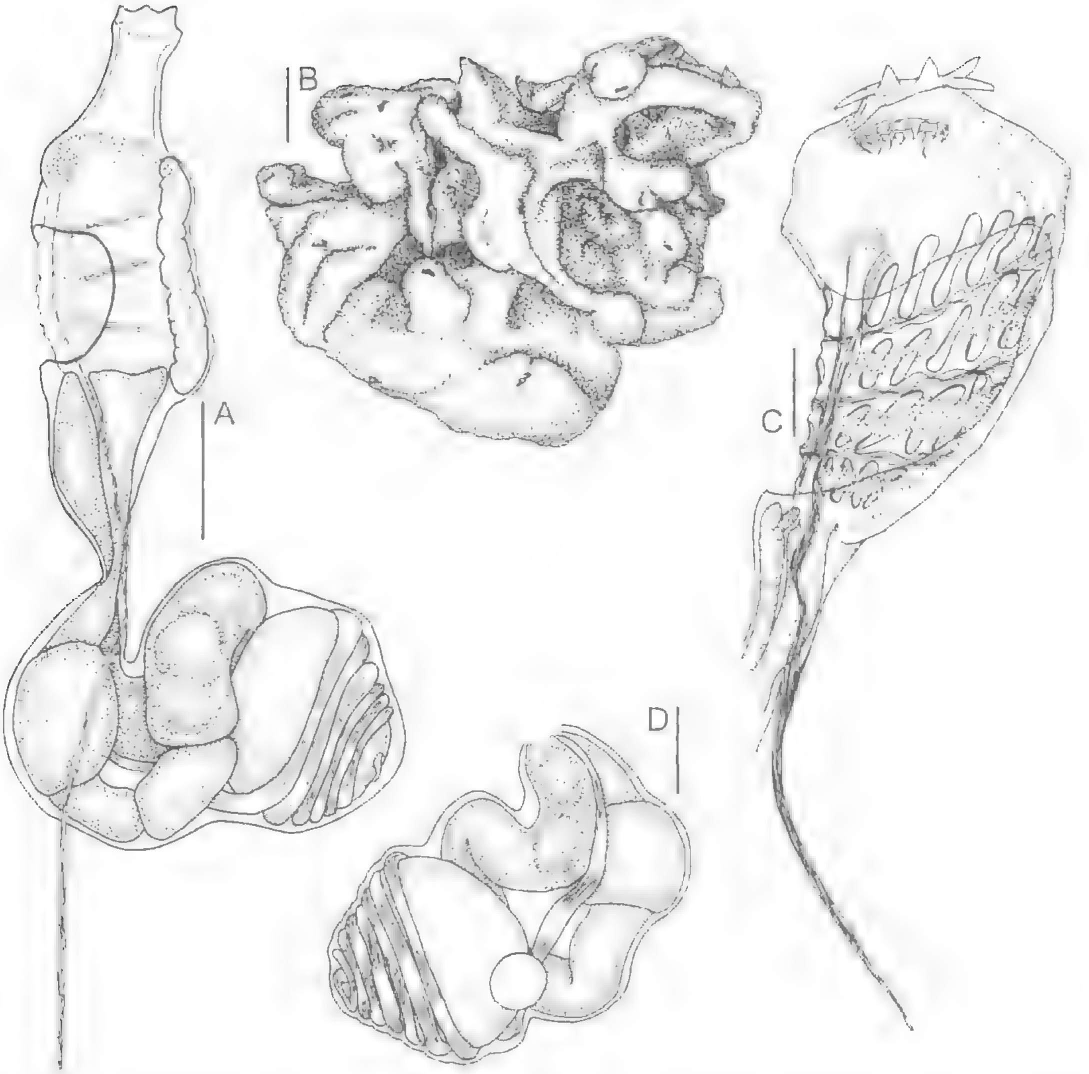


FIG. 96. A, *Didemnum linatum* sp. nov. (WAM 40.89) – A, zooid. B–D, *Didemnum lissoclinum* sp. nov.(B, SAM E2607; C, SAM E2665; D, QM G302879) – B, colony; C, thorax; D, gut and gonads. Scales: A,C,D, 0.1mm; B, 1.0cm.

per row. The atrial aperture is a large sessile opening without an anterior lip. The oesophageal neck is about one-third of the total zooid length, and a well-formed retractor muscle projects from about halfway down the oesophageal neck. The gut loop is bent at right angles to the long axis of the zooids, and the undivided testis has 6 coils of the vas deferens around it.

REMARKS. The large spicules and their sparse distribution, the open horizontal common cloacal cavity with the zooids slung across it in thin test ligaments, the thin layer of basal test and the small zooids without an atrial lip are all distinctive. The vast common cloacal system does resemble that of temperate *D. lissoclinum* which, however, has spicules only half the size of the present species. The spicules are similar in size and form to those of *D. grande*, albeit slightly larger. *D. grande* has deep primary cloacal cavities but some zooid free areas of solid test have zooids embedded around them rather than being suspended in test ligaments that cross an open horizontal cloacal space as they do in the present species. Further, in *D. grande* spicules are

crowded in the central test rather than being confined to a sparse layer in the surface.

Didemnum lissoclinum sp. nov.
(Figs 96B–D, 169G; Pl. 11A,B)

Didemnum turritum: Kott, 1962: 319.
Trididemnum cerebriforme: Kott, 1972b: 178.
Didemnum lambitum: Kott, 1972c: 249 (part, specimen with larvae).

TYPE LOCALITY. South Australia, Great Australian Bight, 32°24'S 113°30'E, 49m, coll. P. Symonds 23.8.73, holotype SAM E2665; Yorke Peninsula, Point Turton jetty piles, 3-4m, coll. K. Gowlett Holmes 31.12.93, paratype SAM E2607.)

FURTHER RECORDS. South Australia (Elliston Bay – SAM E2676, QM G302767; Kott, 1972b; Port Noarlunga – AM Y1528-31 Kott, 1962; Kangaroo I., QM G300981, G302948). Victoria (Mallacoota Inlet, AM Y2318; Deal I., MV10.5). New South Wales (Jervis Bay, QM G302879; Port Hacking, QM G9436, AM Y825).

COLONY. Two colonies (SAM E2607, QM G302767) have narrow cylindrical protrusions from the surface anastomosing with one another to form complex spongy masses, and others (MV 10.5, QM G302879) form open reticula of narrow branches fusing with each other and subdividing. Other specimens (including the holotype) are flat irregular sheets with rounded margins or double-sided fan-shaped lamellae with lobed margins (QM G302948). Branchial apertures are conspicuously stellate, the openings lined with spicules and sometimes slightly depressed into the surface. Sometimes minute spicule-filled papillae are on the surface between the branchial apertures. Spicules are crowded throughout the colony, and the surface is hard and raspy. Spicules are quite large, to 0.07mm diameter, and stellate, with 7–9 and sometimes 11 long conical pointed rays in optical transverse section. The ray length/spicule diameter ratio is about 0.375. The common cloacal cavity is large, deep canals separating the zooids into clumps, and extending posteriorly around the test connectives that attach the clump to the thin basal layer or rod of central test. Thoraces are separated from one another by the thoracic component of the 3-dimensional cloacal system. The surface layer of test is very thin and is depressed over the deep cloacal spaces that surround each clump of zooids.

In life, colonies are pink and beige-tan to cream but are white in preservative.

ZOOIDS. Zooids are small but robust, to at least 1mm overall when contracted. The branchial apertures are short with 6 small points around their rims. The atrial apertures are large exposing most of the branchial sac to the cloacal cavity. An atrial lip was not detected. Four rows of stigmata are in the branchial sac. In 3 colonies (QM G300981, G302769, G302948) it was possible to count 6 stigmata in a row, although usually zooids were too contracted to determine the exact number. A retractor muscle projects into the test from about halfway down the oesophageal neck. A mature undivided almost spherical testis is surrounded by 7 coils of the vas deferens. Small, brownish-pink embryos are in the larval test of specimens collected from Kangaroo I. in January (QM G300981) and Port Hacking in May (AM Y825). The larval trunk is about 0.6mm long, with 4 ampullae on each side of the 3 antero-median adhesive organs. Similar larvae are in *D. turritum*: Kott, 1962.

REMARKS. The paratype superficially resembles colonies of some complex *Trididemnum* species, but in addition to the generic characters which separate these taxa both spicules and zooids are smaller. The outstanding feature of this species is the large common cloacal chamber, with zooids suspended in it in test connectives that connect basal and surface layers of test. It is similar to the cloacal cavities found in certain *Lissoclinum* spp., and in some *Didemnum* spp., (e.g. *D. pellucidum*) from which it is separated by its shorter branchial siphons. *D. membranaceum* has generally similar spicules, but has giant spiky spicules and less extensive cloacal cavities than the present species. *D. delectum* is sympatric and has similar (albeit slightly smaller) spicules and some parts of its common cloacal cavity extending behind the zooids, but it has much smaller zooids than the robust ones of the present species. This species resembles tropical *D. spongioide* in its spicules and 3-dimensional cloacal cavity, although spicules of *D. spongioide* are slightly larger (to 0.078mm diameter) and it has larger, more complex colonies, and smaller, less robust zooids and larvae. *D. microthoracicum* also has similar but larger spicules and more restricted cloacal systems.

The conspecific *D. turritum*: Kott, 1962, differs from other recorded colonies only in the presence (on some parts of the surface) of a pointed papilla over the ventral branchial lobe, which (as in *D. cuculliferum*) appears to close down over the aperture when it is contracted. In these long-preserved specimens (AM Y1528-31), this papilla is small and inconspicuous.

Didemnum macrosiphonium sp. nov.
(Figs 97A–C, 168H)

Didemnum patulum: Kott, 1972a: 18; 1972b: 179; 1976: 65.

TYPE LOCALITY. South Australia (see Kott, 1972a: St Vincent Gulf, Aldinga drop off, 10-25m, coll. S.A. Shepherd 12.12.66, holotype SAM E2657; paratype SAM E2658).

FURTHER RECORDS. South Australia (Kangaroo I. – MV F68758 Kott, 1972b). Victoria (Port Phillip Bay – Kott, 1972a; Western Port – MV F68752 Kott, 1976).

COLONY. Colonies are robust often extensive hard encrusting sheets up to 5mm thick, with spicules packed throughout, especially on the hard rippled base. Zooids are along each side of the deep common cloacal canals that surround elevated zooid-free areas of common test and extend the full depth of the zooids. The lower half of the colony is solid test, not perforated by cloacal cavities. Some fine, irregular branched pigment bodies are amongst the spicules in the surface, especially around the branchial siphons. Spicules outline the stellate branchial apertures (arranged along each side of the slight surface depression over the circular common cloacal canals) and continue down into the siphons. The small (to 0.033mm diameter) spicules are stellate with 9–11, usually conical and pointed but sometimes round- or flat-tipped rays in optical transverse section.

ZOOIDS. Zooids are relatively large, about 2mm long, with a long, muscular, tulip- or vase-shaped branchial siphon that is up to about one-third of the total length of the zooid. Six small pointed lobes are around the rim of the aperture. A narrow atrial tongue projects from the body wall anterior to the sessile atrial aperture. A strong retractor muscle projects from about halfway down the oesophageal neck. About 8 long rectangular stigmata are in the anterior row in the branchial sac. The abdomen is relatively small, the distal part of the gut loop bent up ventrally, to form a double loop. The number of vas deferens coils in this species has not been determined. Larvae are present in a colony collected from Kangaroo I. in January. They are robust, with a trunk 1.0mm long and the tail wound halfway around it. A circle of 26 long ectodermal ampullae surround the 3 antero-median adhesive organs.

REMARKS. The species most resembles *D. elongatum* which has similar cloacal systems, zooids, atrial tongues, long branchial siphons and spicules, although the latter are larger than the present species. The elevated zooid-free areas of solid test surrounded by common cloacal canals with zooids along each side are in *D. grande*, *D. microthoracicum*, *D. patulum*, *D. stragulum*, *D. tonga*) from which the present species is distinguished by its smaller spicules and their diversity, its particularly long and muscular branchial siphon, and relatively large zooids.

Didemnum mantile sp. nov.
(Figs 97D,E, 171D)

TYPE LOCALITY. Victoria (Western Port, Tortoise Head, Southern French I., shallow reef to 6m beside small channel with sea grass very murky, 3m slope, coll. AIMS Bioactivity Group 13.2.90, holotype QM G302881).

FURTHER RECORDS. South Australia (Franklin I. Nuyts Archipelago, SAM E2843).

COLONY. The colonies are hard, tough, leathery encrusting sheets with the surface marked off into small elevated polygonal or oval areas (about 2mm in greatest dimension) by surface depressions over the deep primary common cloacal canals which surround clumps of zooids. The common cloacal cavities penetrate the clump at thorax level. There is some variation in thickness of the basal test.

Branchial apertures are evenly spaced and conspicuously stellate, their margins lined with spicules. They are along each side of the primary canals and zooids in the middle of each clump open in the elevated areas. A thick plug of spicules projects down into the branchial siphon lining. Common cloacal apertures are randomly distributed at the junctions of primary common cloacal canals. Spicules (to 0.045mm diameter with 5–7 long, narrow, pointed rays in optical transverse section) occur throughout the colony. Ray length/ spicule diameter ratio is about 0.4.

Colonies are a dirty whitish-grey colour in preservative and zooids are grey. In life they are described as grey.

ZOOIDS. Zooids are about 1.5mm long. Thorax, oesophageal neck and post-oesophageal end of the gut loop are about equal in length. The branchial siphon is large and funnel-shaped. The atrial aperture is wide exposing most of the branchial sac directly to the cloacal cavity. The branchial sac has 6 stigmata in the anterior row reducing to 5 in the posterior row. Two vascular appendages project from the ventral side of the gut loop. Lateral organs are shallow cups on each side of the thorax. A long tapering retractor projects from the middle of the oesophageal neck. The post-pyloric part of the gut loop is bent up against the stomach to form a double loop. The testis is undivided and has 7 coils of the vas deferens. Larvae are not known for the species.

REMARKS. The species has spicules like those of *D. delectum* but with longer rays and it has tougher colonies with deep primary common

cloacal canals surrounding clumps of zooids and common cloacal apertures at the junctions of the primary canals, rather than the terminal common cloacal apertures of lobed colonies of *D delectum*. *D.clavum* has spicules with long rays most like those of the present species, but the

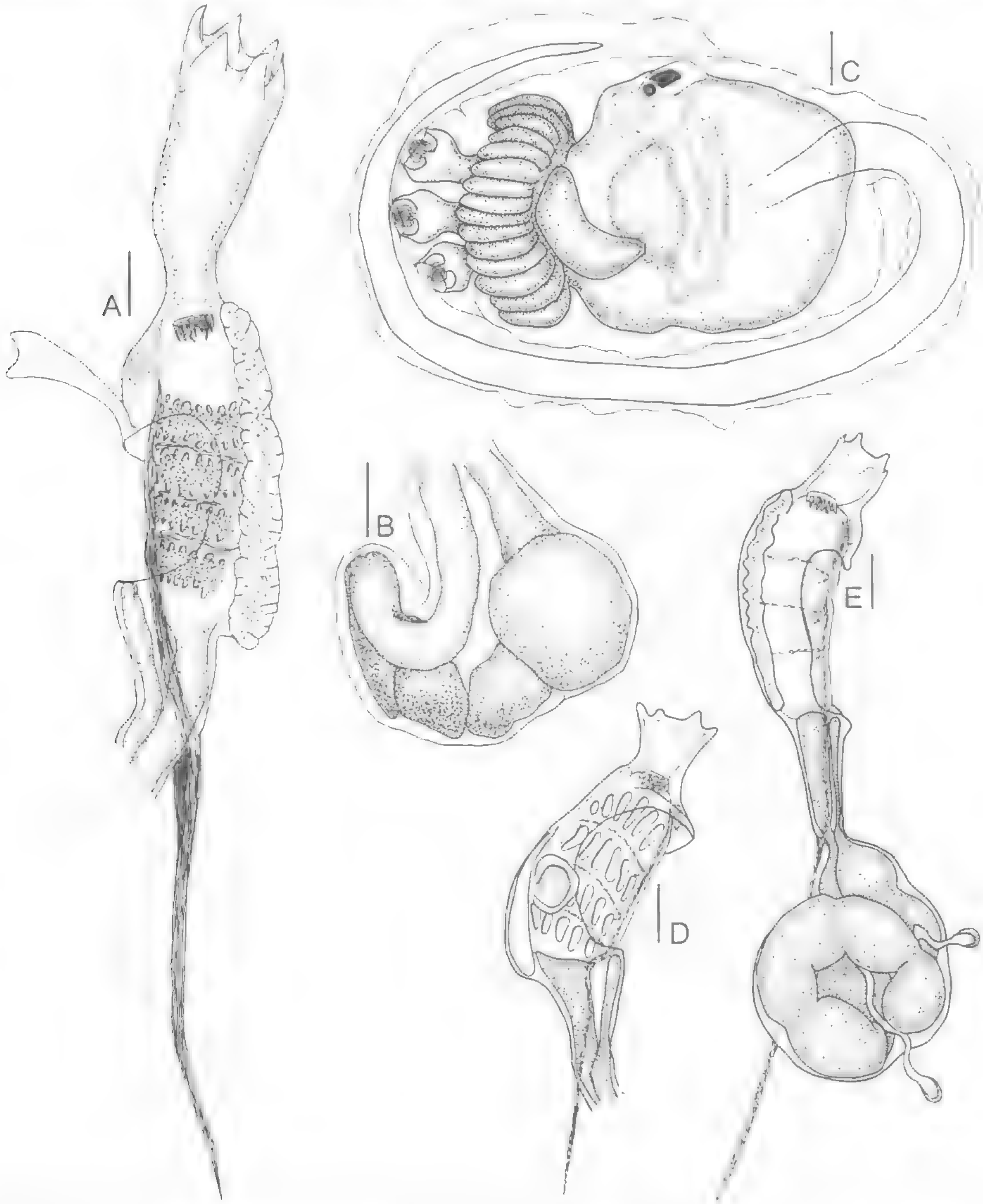


FIG. 97.A–C, *Didemnum macrosiphonium* sp. nov. (A,B, SAM E2658; C, MV F68758) – A, thorax; B, gut loop; C, larva left side with a large horizontal ampulla. D, E, *Didemnum mantile* sp. nov. (D, SAM E2843; E, QM G302881) – D, thorax; E, zooid, showing double gut loop. Scales: 0.1mm.

colonies are different, and *D. clavum* also has occasional giant 4–6 rayed spiky spicules. The tropical *D. verdantum* and *D. etiolum* have similar spicules, but lack the circular canals of the present species, contain symbiotic plant cells in larvae and colonial test and have dark test cells that surround the zooids.

Didemnum membranaceum Sluiter, 1909
(Figs 98, 170D; Pl. 11C–E)

Didemnum membranaceum Sluiter, 1909: 58 (part, specimen ZMA TU471.1 statn 50).
Not *Didemnum membranaceum*: Kott & Goodbody, 1982: 518. Kott, Parry & Cox, 1984: 308. Kott, 1998: 82. Monniot. & Monniot, 1987: 36 (<*D. sordidum*).
Didemnum fraternum Sluiter, 1909: 60.
Didemnum tonga: Kott & Goodbody, 1982: 520.
Didemnum ahu Monniot & Monniot, 1987: 25.
Didemnum moseleyi: Monniot & Monniot, 1996: 157.

NEW RECORDS. Western Australia (Montebello Is., WAM 958.93; Houtman's Abrolhos, WAM 202.87; Dongara, WAM 109.93, 94.95). Queensland (Moreton Bay, QM G308450, G308452; Caloundra, QM G308462, G308490; Heron I., QM G308101, G308123, G308133, G308135, G308138-9, G308165-6, G308169, G308175, G308181-2, G308185, G308207, G308211, G308255, G308338; Swain Reefs, QM G305510, G305558, G305716, G308388-9; Broadhurst Reef, QM G302928; Fantome I., QM GH5363; Davies Reef, QM G308532).Timor Sea (Ashmore Reef, WAM 518.92). Andaman Sea (Similan I., QM G300969.)

PREVIOUSLY RECORDED. Indonesia (lectotype ZMA TU471.1 Sluiter, 1909). French Polynesia (Monniot & Monniot, 1987). Hong Kong (Kott & Goodbody, 1981). Micronesia (Monniot & Monniot, 1996)

COLONY. Colonies form robust but thin investing sheets with large white common cloacal apertures scattered randomly on the surface or sometimes small flat plates each with a central common cloacal aperture and rounded margins (QM G308123, G308166). Many colonies (QM G308123, G308139, G308169, G308181, G308185, G308450, 308490, G308462, G308255) have pointed spicule-filled papillae crowded on the surface between the branchial apertures. Others, including the lectotype (ZMA TU471.1), have rounded papillae crowded on some parts of the surface. In some colonies (QM G308123, G308139, G308165, G308169, G308185, G308207, G308211, G308490) a large papilla is associated with each branchial aperture on some parts or all of the surface. Pigment cells are in the surface, overlying the white spicules that are crowded throughout the test. White opaque spicules form a band around the common cloacal apertures that protrude from the surface. The branchial apertures are evenly scattered over the surface with spicules either crowded around

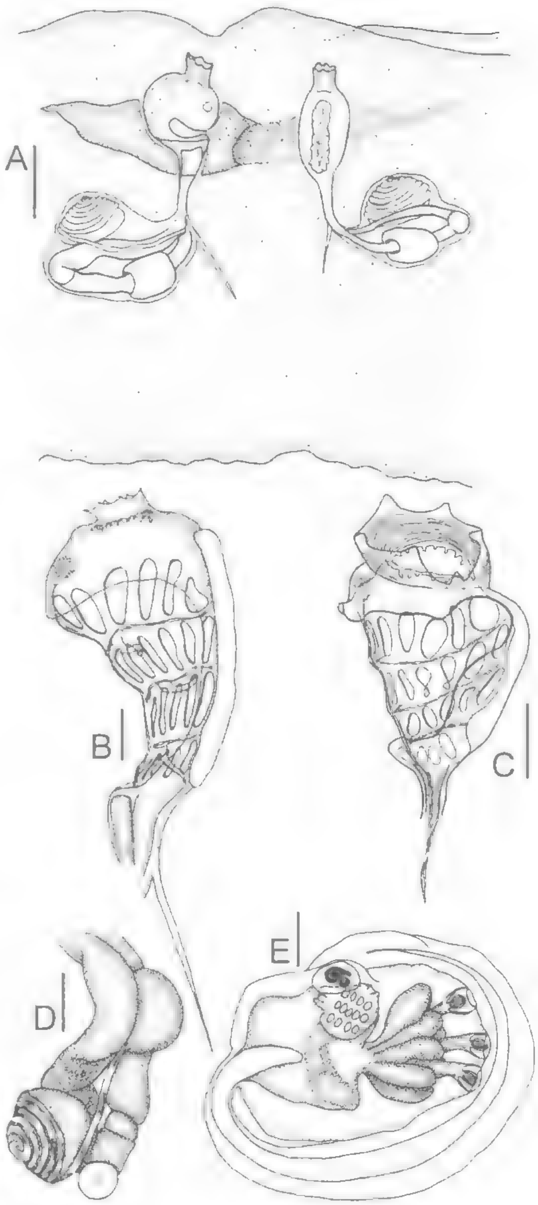


FIG. 98. *Didemnum membranaceum* (A, QM G302928; B,E, QM G308175; C, WAM 518.92; D, QM G308181) – A, semidiagrammatic vertical section through colony; B,C, thoraces; D, gut and gonads; E, larva. Scales. A, 0.2mm; B–E, 0.1mm.

the stellate openings, or lining their margins. In living specimens zooids are orange, yellow, vermilion[R] or flame scarlet[R], and they can be seen through the surface test, where the layer of spicules is thinner over the zooids resulting in the colonies having a spotted appearance. Living

colonies have dragon's blood red[R] pigment cells or clouds of vermilion pigment cells in the surface test. The colour often is affected by the white spicule-filled papillae which, when present, make the red-pigmented superficial test appear pinkish, pinkish-orange, orange salmon[R], flesh[R], strawberry[R], maize coloured[R], geranium pink [R]or vinaceous rufus[R]. In short-term preservative brownish-yellow pigment is present in the test but eventually colonies become white. Zooids are a yellowish brown but also fade to yellow and then white after a period in preservative. The preservative stains yellow to brownish orange.

The cloacal cavity is extensive, principally thoracic, but with deeper primary canals isolating clumps of zooids from one another. The surface layer of test usually is thin. The thoraces cross the cloacal canals in a ventral test sheath that connects the surface to the solid test of the lower half of the colony. In the lectotype (ZMA TU 471.1) the surface of the colony is marked off into groups of branchial apertures by shallow grooves that result from the depression of the surface test over the deep primary cloacal canals. The abdomina, usually embedded in the basal test, are bent at right angles to the vertical axis of the thorax-oesophageal neck, and are twisted up to the right so that the testis (against the dorsal side of the gut loop) is moved up to face the upper surface of the colony.

Spicules generally are up to 0.06mm diameter. Most have 7–11 relatively long, conical, usually pointed, rays in optical transverse section, although in some the rays have blunt tips. The ray length/spicule diameter ratio is about 0.3. Also there are rare but regularly distributed, sometimes giant, spicules to 0.1mm diameter with 4–6 long, narrow sharply pointed rays.

ZOOIDS. Zooids are small, about 1mm long including the testis and the well extended thorax. The posterior end of the thorax is especially narrow and preserved thoraces often are comma-shaped, with a dorsal concavity. The branchial siphon is short. The pointed papilla sometimes associated with a branchial opening accommodates an enlarged ventral branchial lobe. The atrial aperture is wide, exposing most of the dorsal aspect of the branchial sac directly to the cloacal cavity. The thoracic muscles are delicate and the thoraces are well extended in most specimens. The long retractor muscle is free of the oesophagus from a short distance down the oesophageal neck. The anterior 2 rows of stigmata have 6, the next row 5 and the last row has 4 stigmata. The posterior part of the gut loop is flexed up against the anterior part. The relatively small, but almost spherical testis sometimes is slightly pointed on the outside at the proximal end of the vas deferens, which coils 6 times around it. Yellow eggs often are present in the colony.

Larvae are being incubated in the basal test of the lectotype and some of the newly recorded colonies (QM G308169, G308175, G308181, G308185, G308207). The larval trunk is 0.4–0.5mm long, and the tail is wound the whole way around it. There is an ocellus and an otolith, and 4 lateral ampullae along each side of the 3 antero-median adhesive organs.

REMARKS. Apart from the spicules, there is little about this species which distinguishes it from other red encrusting didemnids with red zooids showing through the surface. It has branchial apertures outlined in spicules and spicules crowded throughout the test like *D. candidum*, *D. fragile*, *D. lacertosum*, and *D. perplexum*. Sometimes *D. cuculliferum*, *D. clavum* and *D. perplexum* also have surface papillae associated with the ventral branchial lobes similar to those found in the present species. *D. fragile* and *D. lacertosum* have spicules with more numerous rays that readily distinguish them; spicule rays of *D. perplexum* are conical, but shorter and fewer; and *D. candidum* and *D. cuculliferum* have spicules with fewer, shorter, and more rod-like rays. The giant spicules resemble those of *D. clavum* and *D. cuculliferum* from which it is distinguished by its long pointed conical (rather than rod-like) rays on the majority of stellate spicules. *D. fuscum* has blunt-tipped rod-like spicule rays, lacks the evenly distributed but sparse giant spicules with spiky rays, has 9 vas deferens coils, small larvae with 5 pairs of lateral ampullae (rather than the 4 in the present species), the larval tail is not quite as long, and zooids and larvae are the characteristic brown colour

The 2 specimens originally assigned to this species (ZMA TU471.1, TU471.2) subsequently designated syntypes by Spoel (1969) are not conspecific. Both are extensive encrusting colonies. One (ZMA TU471.1) on a sponge, its surface marked off into areas by the shallow depressions associated with the deep primary canals around each clump of zooids, appears to be the specimen on which Sluiter based this species. It is here designated the lectotype. This specimen has spicule-filled papillae on the

surface, and stellate branchial apertures with marginal spicules. Its spicules are mostly 0.025–0.04mm in diameter (Sluiter, 1909: an average of 0.025mm) with 7–11 conical rays in optical section, and a few spicules to 0.06mm (Sluiter, 1909: 0.055mm) with fewer rays. The other specimen (ZMA TU471.2) is smooth surfaced, lacking both papillae and conspicuously stellate branchial apertures. It has a thoracic cloacal cavity with zooids crossing it in independent test sheaths, and deeper primary canals as in the other specimen. However, its spicules mostly are 0.05–0.1mm in diameter, with 5–7 long rod-like rays in optical transverse section, and it is assigned to *D. clavum*. Sluiter (1909), when describing *D. membranaceum*, overlooked the giant spicules, although he did observe them in the small colonies he assigned to *D. fraternum*. Similar small maize coloured to pink/orange colonies (QM G308166 G308169) taken off *Halimeda*, some with pointed papillae on the surface between the branchial apertures, also belong to the present species.

Specimens from French Polynesia assigned to *D. ahu* Monniot & Monniot, 1987 and those newly recorded as *D. moseleyi* from Micronesia (Monniot & Monniot, 1996) have the same spicules, larvae, coils of the vas deferens, and cloacal systems and are unmistakeably conspecific.

Didemnum microthoracicum sp. nov.
(Figs 99A,B, 172C)

?*Didemnum augusti*: Kott, 1962: 323 (part, specimens from Reevesby I.).

TYPE LOCALITY. South Australia (Avoid Bay, coll. S. Shepherd 10.4.87, holotype SAM E2656).

FURTHER RECORDS. South Australia (? Reevesby I. – Kott, 1962).

COLONY. The holotype is a tough, hard colony, to 0.5cm thick in places, growing around a worm tube. A very thin layer of bladder cells is on the upper surface. Spicules, crowded in the remainder of the test, are large, to 0.09mm in diameter, although they have a great size range and the smaller ones about 0.03mm are relatively common. Spicule rays are long and pointed, the ray length/spicule diameter ratio being about 0.35. Seven to 9 rays are in optical transverse section. Common cloacal cavities are quite restricted canals at thoracic level but occasionally deeper, extending the full depth of the zooids. Zooids line them on each side, with the atrial apertures exposing the branchial sac directly to the canals. The ventral side of the thorax is embedded in the test, and thoraces are not in separate test sheaths. Abdomina are firmly embedded in the basal test.

ZOOIDS. Zooids are very small, less than 1mm overall, with the thorax about half that length. The branchial siphon is short, with 6 shallow points around the rim of the opening. The atrial opening is large and sessile and an atrial lip was not detected. A large vertical oval lateral organ is on each side near the base of the thorax. The long, fine retractor muscle projecting into the test from about halfway down the oesophageal neck is a conspicuous feature of the zooids. Four rows of stigmata are in the branchial sac, with 6 in the anterior row, reducing to 4 or 5 in the last row. The oesophageal neck is long and the gut forms a tight loop. Gonads were not detected in the holotype.

REMARKS. Features of this species are the large spicules with relatively few long, pointed rays, and the small thoraces with a long, fine retractor muscle. *D. delectum* also has small zooids with relatively few, long spicule rays, but they are not as sharply pointed as the present species, spicules are smaller and thoraces are longer and distinctively shaped with a funnel-shaped branchial siphon. The common cloacal systems with relatively narrow canals surrounding zooid-free areas distinguish the present species from *D. lissoclinum* which has similar large spicules but extensive cloacal spaces, the zooids being suspended in them between surface and basal test.

In the tropics, *D. perplexum* has similar but not such large spicules and *D. grande* has equally large spicules with pointed but more numerous rays. Neither have such small zooids nor such limited cloacal systems. The colonies from Reevesby I. (SA) assigned to *D. augusti* by Kott (1962), with stellate spicules to 0.07mm diameter and similar cloacal systems, may be specimens of the present species (see *D. patulum*, Remarks).

Didemnum minisculum sp. nov.
(Fig. 99C; Pl.11F)

TYPE LOCALITY. South Australia (Yorke Peninsula. Stansbury jetty on seagrass 2-3m, coll. K.L. Gowlett Holmes 13.12.94, syntypes SAM E2647.

COLONY. Colonies are small, circular or irregular plates, to 0.5cm in maximum dimension. Some test strands extending out around the perimeter anchor the colony to the substrate. Some of the more irregular colonies appear to be lobulating. Minute white stellate spicules, to 0.03mm in diameter but usually only about

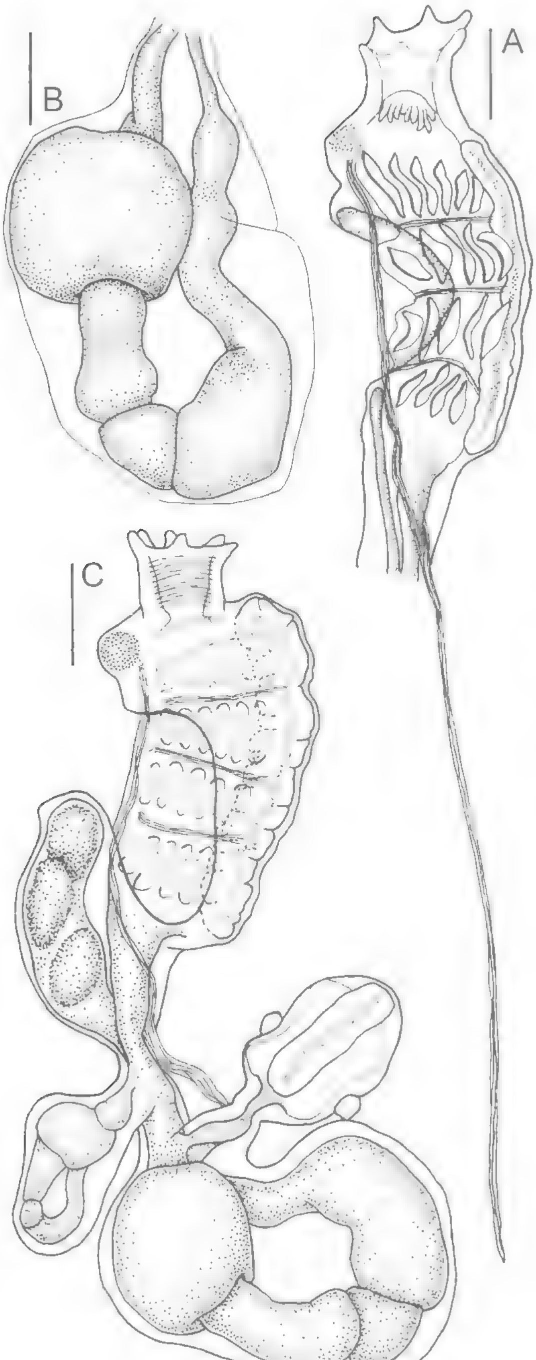


FIG. 99. A,B, *Didemnum microthoracicum* sp. nov. (SAM E2656) – A, thorax; B, gut loop. C, *Didemnum minisculum* sp. nov. (SAM E2647) – C, whole zooid. Scales: 0.1mm

0.01mm have 5–7 conical rays in optical transverse section. They are most crowded around the branchial apertures and in the linings of the siphons, but this could be the result of zooid contraction. Otherwise they are sparsely, but evenly, distributed through the test.

The configuration of the common cloacal cavities was not determined owing to the soft consistency of the test. However, a common cloacal aperture is in the centre of the upper surface, and each colony is a single system.

ZOOIDS. Zooids are small, less than 1mm long. The branchial aperture on a short siphon, is stellate, with 6 pointed lobes around the rim. The atrial aperture is a large sessile opening without an atrial tongue. It exposes most of the branchial sac directly to the cloacal cavity. The retractor muscle projects from the anterior part of the oesophageal neck. The gut, divided into the usual stomach, duodenum, posterior stomach and rectum forms a simple loop. Only a few zooids are sexually mature, with an undivided testis and 6 coils of the vas deferens. Larvae are not known.

REMARKS. The small lobulating colonies and minute zooids resemble tropical species with prokaryotic symbionts, viz. *Diplosoma virens* *Didemnum etiolum*, *D. flavoviride* and juvenile *D. molle*, both in colony shape, holdfasts anchoring them to the substrate and the soft test. The present species does not appear to contain any symbionts. The colonies are very inconspicuous, and it is not surprising that it has not been recorded previously. The zooids are possibly the smallest *Didemnum* zooids yet recorded.

D. effusium differs in being completely aspicular, having 10 coils of the vas deferens and the retractor muscle projecting from the relatively large zooids near the base of the oesophagus.

Didemnum molle (Herdman, 1886)
(Figs 100A-C, 166C; Pl. 11G,H)

Diplosomoides molle Herdman, 1886: 310. Sluiter, 1909: 85; 1913: 78.
Didemnum molle: Kott, 1980: 2; 1981: 169; 1982a: 98; 1998: 82. Bachmann et al., 1985: 1211 (part, colonies with *Prochloron* only). Millar, 1988: 829. Lafargue & Vasseur, 1989: 64. Monniot & Monniot, 1996: 157.
Not *Lissoclinum molle*: Tokioka, 1967: 95 (<*Lissoclinum bistratum*). Kott, 1977: 618 (<*Lissoclinum bistratum*). Newcomb & Pugh, 1975: 533 (<*Lissoclinum punctatum*).
Didemnum ternatanum: Van Name, 1918: 152. Tokioka, 1955: 47; 1967: 77. Tokioka & Nishikawa, 1975: 326. Kott, 1966: 287; 1977: 618. Vasseur, 1970: 213. Newcomb & Pugh, 1975: 533. Millar, 1975: 229.

Not *Didemnoides ternatanum* Gottschaldt, 1898: 648. Hartmeyer, 1909-11: 1451.
Not *Didemnum ternatanum*: Kott, 1972a: 179.
Didemnum sycon Michaelsen, 1920: 44.

NEW RECORDS. Western Australia (Kimberley, WAM 769.91; Lacepede Archipelago, WAM 962.89; Dampier Archipelago, WAM 1062.83; Shark Bay, WAM 1060-1.83; Houtman's Abrolhos, WAM 201.87; Esperance, WAM 1152.88). Queensland (Swain Reefs, QM G305708; Broadhurst Reef, QM G300964, G300996 G302915, G302944, G308482; Bowden Reef, G302921; Tydeman Reef, QM G302895; Shelburne Bay, QM G308534).

PREVIOUSLY RECORDED. Northern Territory (Darwin – Kott, 1966. Western Australia (Cockburn Sound – Kott, 1977). Queensland (Heron I., Lewellyn Reef – Kott, 1980; Lizard I. – QM G9780 Kott, 1980; Martha Ridgeway Reef, Deltaic Reef, Raine I. – Kott, 1982a). Western Pacific (Solomon Is – Kott, 1980; Philippines – AMNH Chordata 2138-40, USNM 2988 5982 6339 7384 Van Name 1918,USNM 11404 Tokioka, 1967, Millar, 1975, Kott, 1980 1982a; Aru I. – BMNH 87.2.4.446 Herdman, 1886, Sluiter, 1913; Solomon Is – Kott, 1980; Indonesia – Sluiter, 1909, Millar, 1975; Okinawa – Tokioka & Nishikawa, 1975; Palau Is – Tokioka, 1955 1967, Kott, 1980; Caroline Is – Kott, 1980 1982a; Guam – Kott, 1982a; Fiji – Kott, 1981 1982a; Vietnam – Monniot & Monniot, 1996). Indian Ocean (Zanzibar, Malagasy, Maldives – ZMH K1088-9 syntypes *D. sycon* Michaelsen, 1920, Vasseur 1970, Bachmann et al., 1985, Larfargue & Vasseur 1989; Seychelles – Monniot & Monniot, 1996).

The species is known mostly from low tide down to 40m (Van Name 1918) on sea grass, coral and rocky substrates, in lagoons and in other relatively protected habitats where it is not exposed to strong currents or turbulence which could damage these delicate colonies. However it is affected by light, its obligate *Prochloron* symbionts precluding its ability to accommodate low light intensity, and records of its occurrence at depths below 20m are rare. Sluiter's (1909) record to 69m is unusual and it is probable that it was particularly clean water, as green plants usually do not grow below about 30m.

The geographic range of this species is vast — from the western Indian Ocean to Fiji, and from Okinawa to the southern Great Barrier Reef, Cockburn Sound and Esperance (WA) — from almost 30°N to more than 30°S and through the Indo-West Pacific tropical coralline region. This range is particularly remarkable in view of the usually short (up to 10 minutes: Olson, 1983) free swimming larval life. It is concluded that gene flow occurs not only through chains of recruitment around continents and along chains of islands and reefs, but also that populations are transported over appreciable distances by drifting objects, otherwise deeper oceanic waters would isolate populations from one another. Nevertheless, it should be noted (Olson, 1983) that metamorphosis is delayed when there are no shaded places to provide a stimulus to settle (e.g. open oceans, or night time). Thus gene flow over middle distances could occur through larval recruitment following delayed metamorphosis (Kott, 1980). The new record from Esperance is the most southerly and its spread into the Southern Ocean around the SW corner of the continent could be by the southwards flowing Leeuwin Current.

COLONY. Colonies are a dome-, barrel- or irregular vase-shape each with a terminal common cloacal aperture. Juvenile colonies are flat, and predominantly green, the *Prochloron* in the common cloaca clearly seen, the minute spicules being only in small groups around each branchial aperture. Often colonies (including holotypes of *D. molle* and *D. sycon* from the western Indian Ocean) are up to 10cm in diameter. Usually only smaller colonies (1–2cm diameter) are found in shallow tropical waters.

Colonies are attached to the substrate by fine strands of spicule-filled test that project from around the base. The outer surface is smooth and even. Superficially, a very thin layer of bladder cells overlies a thin layer of small (to 0.025mm diameter) globular spicules, burr-like, with crowded, cylindrical, flat-tipped rays. Spicules are not present in the soft internal test. Stellate branchial apertures are visible on the surface of the colony, with spicules continuing down into the siphon lining.

The colour of living colonies is very variable — from almost white, to light or dark grey with or without patches or strips of brown, light to dark brown, or occasionally purple or even almost black. Pigment is in spherical, oval or irregular pigment cells present superficially, or beneath the spicules or mixed with them in the surface layer. The colour and its intensity usually is a result of the concentration of both pigment cells and spicules, more intense colour being associated with less crowded spicules or with the presence of pigment cells in significant concentrations in the superficial test above the spicule layer. When present in the superficial layer of test the pigment cells are compressed into irregular fusiform or stellate shapes between the bladder cells to form a three-dimensional trabecular pattern.

Each colony has a central test core surrounded by an extensive common cloacal cavity. The central core is attached to the surface zooid-bearing layer by radial connectives crossing the cloacal cavity. Symbiotic *Prochloron* cells can be seen lining the common cloacal cavity of living colonies. When disturbed these colonies generate a massive amount of mucus, which is liberated from the common cloacal aperture together with *Prochloron* cells from the layer lining the cavity.

ZOOIDS. Zooids are up to 1.5mm long. Branchial apertures are stellate, with 6 pointed lobes around the rims. The atrial aperture is wide

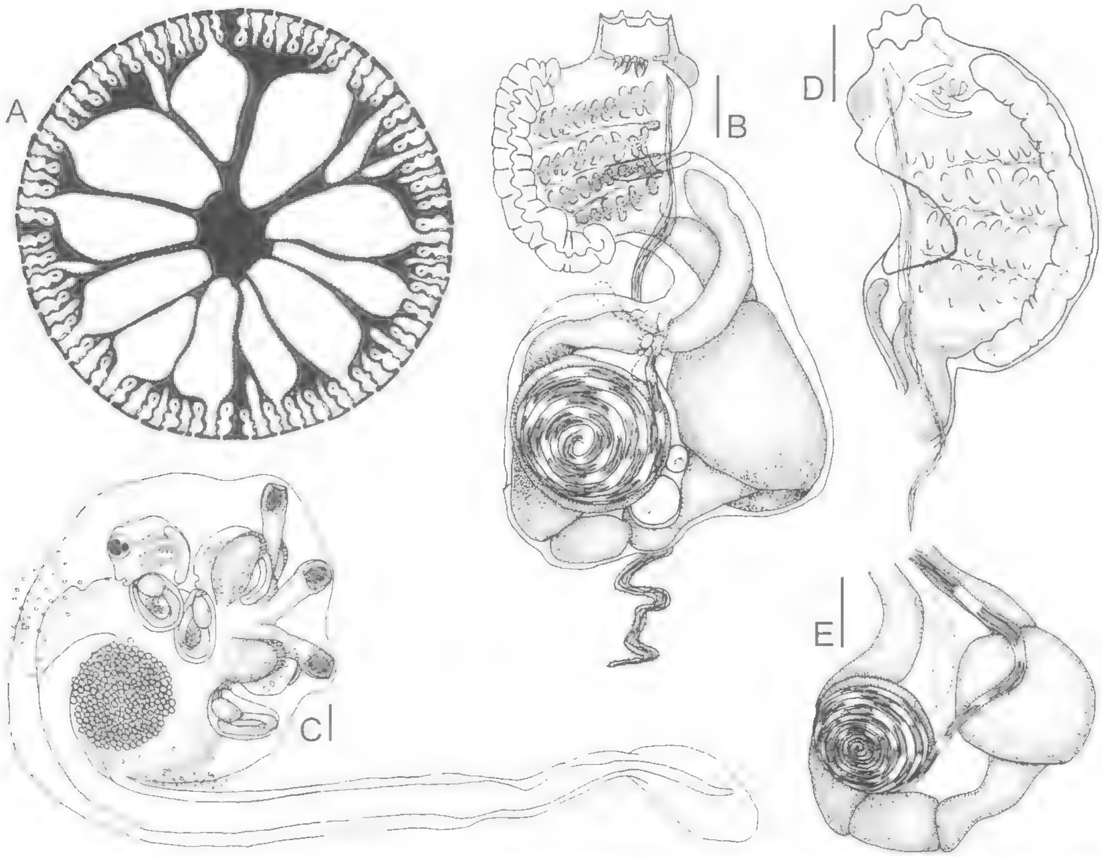


FIG. 100.A–C, *Didemnum molle* (QM G9780) – A, diagrammatic horizontal section through colony (dots lining common cloacal cavities indicate location of symbionts); B, zooid from left side; C, larva. D,E, *Didemnum moseleyi* (QM G308403) – D, thorax; E, gut loop and testis dorsal view. Scales: 0.1mm.

exposing most of the perforated pharynx directly to the cloacal cavity. An atrial lip is not present. A pointed retractor muscle projects postero-ventrally from the postero-ventral part of the thorax. The thorax is wide, with 8–10 stigmata per row. The gut has an almost spherical stomach, long duodenum with slight expansion distally, an oval posterior stomach, and the rectum — constituting the long ascending limb kinked up ventrally over the testis. Seven coils of the vas deferens surround the outside of the undivided testis.

Larvae are found being incubated in the central test of specimens taken in June, August and December. Kott (1982a) observed that larvae are found free in the cloacal cavity prior to their release from the colony (see Olson, 1983). The species is prolific and a large number of embryos are produced by each colony.

Larvae are large, with a deep trunk to 0.09mm long and a tail wound about three-quarters of the way around the trunk. The oozooid is about halfway along the larval trunk. Two blastozooids develop in the trunk — abdominal buds at the right and thoracic ones on the left. An ocellus and otolith are in the cerebral vesicle. Two long lateral ampullae are on each side of the 3 antero-median adhesive organs. A cap of modified columnar cells is on the tip of each ampulla. The test over the conspicuous haemocoel, at the posterior end of the larval trunk, is divided into hair-like strands in which *Prochloron* are entangled. This is the part of the larval trunk that will in due course be overgrown by the developing colony to form the cloacal cavity. Thus *Prochloron* from the parental common cloacal cavity is transported to inoculate the new generation colony (Kott, 1980, 1982a).

Kott (1982a) documented the early stages in colony development following larval settlement. Growth rate is rapid, reflected in the development of blastozooids in the larva, and the active process of replication that can be observed in adult colonies, where oesophageal buds usually are present.

REMARKS. The species is readily identified by its colony form, small spicules, presence of *Prochloron*, and the massive amounts of mucus generated by living colonies whenever disturbed.

The extensive geographic range, dramatic size range and colour variations recorded, suggest that more than one species may be involved. Kott (1982a) noted a difference between the newly metamorphosed colonies of highly pigmented and 'white' parental colonies. No other morphological differences have been detected in either larvae or zooids. Nevertheless there may be a genetic difference of specific significance, for the known colour variants occur sympatrically. The early juvenile colonies of other colour variants have not been investigated.

Kott (1980) discussed synonymy of this conspicuous component of the Indo-West Pacific tropical fauna, and one of the best studied of the didemnid-algal symbioses. It is an obligate symbiosis — death results from the occlusion of light (Bachmann et al., 1985). Colonies without symbionts from deeper water (40m) which the latter authors believed to be conspecific are a different species, possibly *Atriolum marinense* which has a similar small flask-shaped colony, often with some green symbionts on the surface, which could be mistaken for the present species.

Didemnum monile sp. nov.
(Fig. 167H)

TYPE LOCALITY. South Australia (Nuyts Archipelago just north of centre of West I., sand and seagrass beds, coll. P. Aerfeldt et al., 14.9.83, holotype SAM E2683).

COLONY. The colony consists of soft almost spherical lobes, each about 1cm diameter, attached to a weed stalk and joined to one another by thin strips of test fixed along the substrate. Spicules in the surface test are mixed with bladder cells giving the colony a fluffy appearance. Branchial apertures are surrounded by spicule-free areas but small spicules are in the linings of the siphons and, from the surface, appear to outline the stellate apertures. Spicules are less crowded in the central test of the spherical lobes. Spicules are particularly small, to 0.02mm in diameter, with 11–13 long club-shaped, pointed or almost fusiform rays in optical transverse section. The ray length/spicule diameter ratio is about 0.35.

The common cloacal cavity is shallow and thoracic, surrounding the central test mass. Brown pigment is dispersed throughout the test and can be seen through the open branchial apertures conferring a dirty brown colour to the preserved material.

ZOOIDS. Zooids are minute, the contracted thorax being about 0.25mm long. The branchial siphon is short with shallow lobes. The retractor, from the posterior end of the thorax is thick and stumpy in the holotype. The sessile atrial aperture is wide open. Four rows each of about 6 stigmata are in the branchial sac, although the exact number in these contracted zooids was not determined. The abdomen is small, the gut forming a compact loop. Gonads were not detected. Larvae are not known.

REMARKS. The species is distinguished by its small zooids, spherical colony lobes, minute spicules with relatively numerous long rays, and small zooids. Despite the lack of gonads the small zooids with distinct retractor muscle are assigned to *Didemnum* rather than *Polysyncraton*, the latter usually having an atrial tongue and larger zooids than the former. Of known temperate species of *Didemnum*, one with similar colonies formed of fleshy spherical lobes joined by thin strips of test is not known. *D. fragum* with an upright conical colony has spicules crowded at the surface, and they become less crowded in the central test mass, but it has a 3-dimensional cloacal cavity and larger spicules with shorter conical rays. Other species have sheet-like colonies, usually with spicules crowded throughout.

The long spicules rays of the present species that help to distinguish it, are like some in *D. psammatode*, however the present species lacks the spicules with shorter conical rays that also occur in *D. psammatode*.

Didemnum moseleyi (Herdman, 1886)
(Figs 100D,E, 168D)

Leptoclinum moseleyi Herdman, 1886: 272.
Didemnum moseleyi: Sluiter, 1909: 45; 1913: 74. Van Name, 1918: 151. Tokioka, ?1949b: 43; 1954: 243; 1955: 44; 1961: 106; 1967: 65; 1970: 52. Kott, 1957: 136; 1962: 328; 1998: 82 (part, Indo-West Pacific tropical records only).
Not *Didemnum moseleyi*: Kott, 1972a: 19; 1972b: 179; 1976: 65 (<*D. incanum, D. vulgare*). Eldredge, 1967: 210 (<*D. cuculliferum, Trididemnum* sp. and ? *D. candidum*). Monniot & Monniot, 1996: 157 (<*D. membranaceum*).

NEW RECORDS. Queensland (Capricorn Group, QM G308039, G308043).

PREVIOUSLY RECORDED. Queensland (Currumbin, Caloundra, Mooloolaba, Yeppoon, Mackay – Kott, 1962). Indian Ocean (Gulf of Suez, Kott, 1957). West Pacific (Indonesia – Sluiter, 1909 1913; Philippines – holotype BMNH 1887.2.4.404-7 Herdman 1886, Van Name 1918, Tokioka, 1967 1970; Palau Is – Tokioka, 1955 1967; New Caledonia – Tokioka, 1961; Tokara Is – Tokioka, 1954; Fiji – Kott, 1981).

The present species appears to have a range through the Indo-West Pacific. However, many of the tropical records and most of the temperate ones require revision and are not included in the synonymy nor discussed in this work.

COLONY. Colonies form extensive thin but robust encrusting sheets. They are hard, with spicules crowded throughout. Most colonies (including the holotype) are smooth without papillae on the surface. Sessile common cloacal apertures, randomly distributed over the surface, have their rims divided into 5 lobes, each with a radial rib of spicules continuing into the roof of the cloacal cavity.

Living specimens sometimes have red or madder brown[R] pigment forming a reticular pattern where its distribution is interrupted by minute clumps of crowded spicules. The zooids are a darker colour and show through the spicules in the surface. Branchial apertures are conspicuous where white spicules are crowded in the siphonal linings, and outline the stellate apertures. In one specimen (QM G308039) there is some purple pigment mixed with spicules around each zooid, making purple marks on the surface. Some brown pigment often is embedded in the surface test of the preserved colonies.

Spicules are to 0.05mm in diameter, with up to 11 rays in optical section. These vary in shape, some having pointed conical rays, while others have round-tipped rays, and some are almost globular with flat-ended rays that barely project from the central mass.

The cloacal cavity is thoracic, interrupted by thoraces of the zooids crossing it, each with a separate ventral sheath of test joining the relatively thick surface test to the thicker basal layer. Abdomina are not always completely embedded in the basal test, and they sometimes project up into the common cloacal cavity.

ZOOIDS. Zooids are robust. The branchial siphon is relatively short and cylindrical. The branchial sac has 8 stigmata in the anterior row, although stigmata in the more posterior rows could not be counted. The atrial aperture is sessile. An atrial tongue was not detected. The gut loop has the usual long duodenum and round posterior stomach. The rectum is wide proximally and the distal end of the gut loop is flexed ventrally over the testis. The testis has 9 coils of the vas deferens around its outer half. A strong retractor muscle projects from a short distance down the oesophageal neck.

Larvae were not detected in either newly recorded specimens, or the holotype, or from Fijian and Hong Kong specimens. Kott (1962) and Tokioka (1967) described larval trunks as, respectively, 0.4mm and 0.55mm long, with 4 pairs of lateral ampullae, although neither author identified the colony or location from which each larva came.

REMARKS. The species has short, cylindrical branchial siphons (Herdman, 1886, pl.37, fig. 10) and hard, firm colonies that contribute to species diagnosis. However, its most useful distinguishing characters are its spicules. Re-examination of the holotype, BMNH 1887.2.4.404-7, has confirmed the characteristic variations of the spicule rays that can be used to distinguish the species. The type specimen is in good condition, although what was a single colony now consists of 7 pieces — 5 pieces and another 2 dissected fragments (in a vial).

D. elongatum has similar spicules to the present species but different cloacal systems with zooids embedded along each side of deep circular primary cloacal canals and zooids with an atrial lip and long branchial siphons. The species has similar but larger spicules and the same number of vas deferens coils as *D. diffundum* Monniot, 1995 from New Caledonia (see also *D. apuroto*: Monniot & Monniot, 1996) but that species has more complex colonies with ramifying lobes and terminal common cloacal apertures. *D. apuroto* Monniot & Monniot, 1987 (Monniot, 1995) has similar but smaller spicules and its colonies are thin, white crusts rather than extensive sheets.

The spicules with blunted and round-tipped rays that Eldredge (1967) referred to as 'typical', are not characteristic — the present species has a mixture of globular, stellate and mulberry like spicules. Most specimens from the western Pacific he assigned to *D. moseleyi* may be *D. candidum*. One (from Eniwetak) with rare 'slender-rayed tetrahedral spicules' (Eldredge, 1967: 212) probably is *D. cuculliferum*; and dark-coloured abdomina of other specimens suggest the dark squamous epithelium of a *Trididemnum* sp.

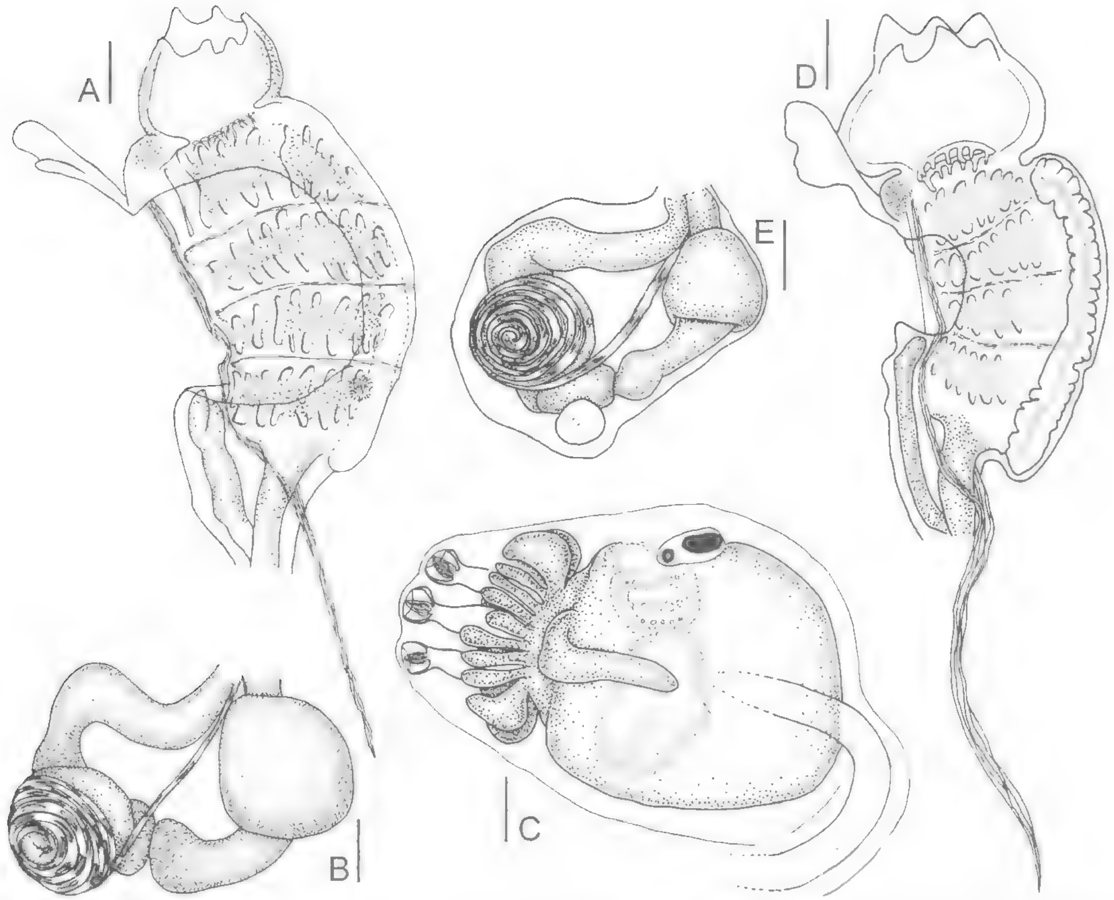


FIG. 101.A–C, *Didemnum multispirale* sp. nov. (A,B, QM G308188); C, ZMA TU454.3) – A, thorax; B, gut loop and testis; C, larva from left showing large horizontal ampulla. D, E, *Didemnum mutabile* (QM G308205) – D, thorax; E, gut loop and gonads. Scales: 0.1mm.

Didemnum multispirale sp. nov.
(Figs 101A–C, 166 I; Pl.12A,B)

Didemnum albopunctatum Sluiter, 1909: 58 (part, ZMA TU433.3).
Didemnum digestum Sluiter, 1909: 54 (part, ZMA TU442.1).
Didemnum jedanense Sluiter, 1909: 59 (part, ZMA TU454.3).

TYPE LOCALITY. Queensland (Heron I., eastern end of reef, under surface of rubble, 0.5m, coll. P. Kott et al., 9.3.93, holotype QM G308017, paratype QM G308044).

FURTHER RECORDS. Western Australia (Exmouth Gulf, WAM 1003.89). Queensland (Capricorn Group, QM G302046, G308141, G308146, G308155, G308188, G308313, G308333; Swain Reefs, QM G305626, G305805, G308390, G308392, G308414, G308434; Bowden Reef, G302920; Orpheus I., QM G300990, G308643; Stanley Reef, QM G308489; and Lizard I., QM G300962). New Caledonia (Monniot, 1995). Indonesia (ZMA TU454.3 Sluiter, 1909).

COLONY. Colonies are irregular, narrow, sheet-like or slightly lobed encrusting sheets. Usually, spicules are packed throughout the test and continue down into the siphon lining, sometimes outlining the margins of the stellate branchial apertures and often forming a white plug in the siphon (which makes it difficult to remove the entire zooids from the test). Primary cloacal spaces are deep, surrounding clumps of zooids, and they extend to abdominal level, leaving a thin basal test under the cloacal cavity and depressions around polygonal elevations on the surface of the colony. There is never a superficial bladder cell layer and spicules are crowded at the surface making it hard. Shallow, secondary common cloacal spaces penetrate amongst the thoraces in each clump, leaving each thorax isolated in a separate test sheath. The various colours reported for living colonies are flesh colour[R], vinaceous rufus[R], vinaceous red[R], coral red[R], beige[R], bright orange[R], or mottled flame scarlet[R] and saturn red[R], or coral red[R], with

white dots where plugs of white spicules are in the branchial siphon. However in photographs colonies are some shade of orange or red-orange, with variable yellow patches between the zooid openings and white-rimmed common cloacal openings. Living zooids are burnt carmine[R], vermilion[R], flame scarlet[R] to orange. Colonies and zooids are white in preservative and orange pigment accumulates in the depressions that surround the elevated clumps of zooids. Often a reticular pattern develops where spicules clump together with diffuse red pigment between. White rims around common cloacal apertures result from the absence of pigment and presence of spicules, although a ring of darker pigment often is present outside the white rim. White spicules in the floor of the cloacal cavity are seen through the open cloacal apertures. Patches of algal cells (probably Chlorophyta rather than *Prochloron*) sometimes are present on the surface.

Spicules are moderately large, generally to 0.05mm, but occasionally up to 0.09mm (QM G308017) in diameter. The majority have 15–19 short, pointed conical rays sometimes with forked tips in optical transverse section. Others, usually smaller than the stellate ones, are globular with flat-ended rays. Bases of the conical rays are separate from one another on the central spicule mass.

ZOOIDS. Zooids are relatively large, to about 1.5mm long. The abdomen usually is bent up at right angles to the thorax. The branchial siphon is relatively large and muscular with 6 small, pointed lobes around the rim, a well developed sphincter muscle around its base and usually a plug of white spicules which stretches it to a balloon-like shape. The atrial aperture is large, exposing most of the branchial sac to the cloacal cavity. An atrial tongue, often long, narrow, and bifid at its distal end, is on the anterior rim of the opening but this often is torn when the zooid is removed from the test.

The branchial sac has about 10 or 11 stigmata per row in the 3 anterior rows, and 8 in the last row. A robust retractor muscle of variable length projects from about halfway down the oesophageal neck. The gut loop has the proximal part of the ascending limb looped up to accommodate the large almost spherical testis follicle that lies beneath it. The vas deferens makes 9 coils around the outer half of the testis.

Larvae are present in the colony from Indonesia which Sluiter (1909) had assigned to *D. jedanense* (ZMA TU454.3). They have a deep larval trunk 0.7mm long with 10 lateral ampullae along each side of the 3 antero-median adhesive organs and the tail wound two-thirds of the distance around the trunk. Blastozooids were not detected. A large horizontal ectodermal ampulla is on the left, reaching from the waist behind the lateral ampulla to the middle of the larva trunk.

REMARKS. The species is distinguished by its large branchial siphon, the origin of the retractor muscle from halfway down the oesophagus, the two relatively uniform spicule types packed throughout, and the wide, flat testis with numerous vas deferens coils. The red-orange-yellow colonies are also characteristic. *D. levitas* has similar spicules, zooids and larvae. However, its spicules are in a surface and basal layer (not between) and have 17–19 rays in optical transverse section, its colonies are thin with the basal test penetrating into recesses in the calcareous substrate and zooids have only 7 coils of the vas deferens. *D. mutabile* Monniot & Monniot, 1987 has a large branchial siphon and similar stellate spicules, although globular ones do not occur, and its larval trunk is smaller than that of the present species with only 5 pairs of ectodermal ampullae. Spicules are a similar size to those of *D chartaceum* but the conical spicule rays are fewer, longer, and not as crowded. Unlike *D. chartaceum* (which has bladder cells throughout the colony and only 2 layers of spicules — one on the base and one near the surface), the present species generally has spicules crowded throughout. Further, in *D. chartaceum* zooids are smaller and colonies become darker in preservative rather than white.

The larvae with their deep trunk, and numerous lateral ampullae resemble those of *D. arancium* (> *D. ligulum*: Monniot & Monniot, 1987, part, orange colonies), *D. chartaceum*, *D. jedanense* and *D. precocinum* but all 4 species have a larval blastozooid, different spicules and other aspects of their zooids and colonies that distinguish them.

The present species has a similar but smaller larval trunk than *D. ligulum* Monniot, 1983 from the tropical western Atlantic, and lateral ampullae are more numerous in the latter species. Further in specimens from Guadeloupe the spicules have shorter conical rays and the cloacal cavities are posterior abdominal.

The flat rose-coloured colonies also assigned to *D. ligulum*: Monniot & Monniot, 1987 have similar but smaller larvae than the present species and similar spicules with pointed and blunt-tipped rays but the rays are longer and more

numerous. Further, these rose-coloured specimens have distinctive colonies with discrete systems isolated from one another by solid walls of test (as in *Polysyncraton glaucum*). They appear to be an undescribed species. *D. ligulum*: Monniot, 1995 from New Caledonia is a distinct species (*D. ossium* below) with more numerous larval ectodermal ampullae.

Didemnum mutabile Monniot & Monniot, 1987
(Figs 101D,E, 167A)

Didemnum mutabile Monniot & Monniot, 1987: 37.

NEW RECORDS. Queensland (Heron I., QM G308205).

PREVIOUSLY RECORDED. French Polynesia (Moorea, Tahiti – Monniot & Monniot, 1987).

COLONY. Although the French Polynesian type material consisted of small thin orange plates, the newly recorded colony is a hard, narrow irregular strip, about 3cm long, a dirty beige colour in life and white in preservative. It lacks a spicule-free superficial layer of test, and the colony has a raspy surface.

Spicules (to 0.06mm diameter) are crowded throughout. They are stellate, with 17–19 short conical, pointed rays in optical transverse section and are remarkably uniform. The bases of the spicule rays are not crowded together, and are separated from each other on the central spherical mass of the spicule. Plugs of spicules are present in the branchial siphon. The common cloacal canal is shallow and thoracic with zooids crossing it in test sheaths crowded with spicules.

ZOOIDS. Zooids are relatively small when contracted, although the branchial siphon remains large and turnip-shaped, often of greater diameter than the thorax. Its shape is maintained by the clumps of spicules in the test that turns in to line the siphon. Six small sharply pointed lobes surround the rim of the branchial opening. The atrial aperture is a relatively limited sessile opening with a lip of variable length, sometimes bifid at the tip, but often inconspicuous, projecting from the anterior rim of the opening. The branchial sac has about 7 stigmata in the anterior row, although these could not be counted accurately. A conspicuous, strong, retractor muscle projects from the upper part of the oesophageal neck although in contracted zooids it appears to project from near the posterior end of the thorax. The gut forms a circular loop. The testis is surrounded by 7 coils of the vas deferens.

Larvae are not in the new specimen but in the type material (Monniot & Monniot, 1987) have a trunk about 0.3mm long, with 5 pairs of ectodermal ampullae, and the tail is wound almost the whole way around it.

REMARKS. The large turnip-shaped branchial siphon, filled with a plug of spicule-filled test also occurs in *D. multispirale*, which also lacks a bladder cell layer, but is distinguished by the fewer rays on the stellate spicules, some globular spicules, 9 coils of the vas deferens and 10 larval ectodermal ampullae. *D. levitas* also has 7 coils of the vas deferens, a similar branchial siphon, and 17–19 spicule rays in optical transverse section. It is distinguished by the absence of spicules from the middle layer of the test and by its more numerous larval ectodermal ampullae. *D. ossium* and *D. bicolor* also have large turnip-shaped branchial siphons, but they have a greater diversity of spicules including stellate ones with long, pointed rays.

Although zooids of the newly recorded specimen are not smaller than those generally occurring in this genus Monniot & Monniot (1987) described the zooids of the type material as particularly small (0.6mm long). However, the zooids they figure (Monniot & Monniot, 1987, fig. 11A-E) have very contracted thoraces, except for the branchial siphon which is the characteristic shape, probably prevented from contracting by its plug of spicules.

Didemnum oblitum sp. nov.
(Figs 102,165-I)

TYPE LOCALITY. Queensland (Swain Reefs, Price Cay west side 20m, coll. S. List 26.7.95, holotype QM G308380; Gannet Cay 25m, coll. S. List 24.7.95, paratype QM G308363; Thomas Cay 30m, coll. S. List 29.7.95, paratype QM G305733; Frigate Cay 20m, coll. S. List 27.7.95, paratype QM G305605; Price Cay SW side, 20m, coll. S. List 26.7.95, paratype QM G308386).

FURTHER RECORDS. Queensland (Hervey Bay, QM G308472; Swain Reefs, QM G308387, G308400, G308403, G308428).

COLONY. In life colonies are thin, slate-coloured, irregular sheets growing over coral rubble. White spicules are mixed with black pigment in the surface test. Black pigment seems to be concentrated around the branchial apertures. Spicules are absent around the rims of the cloacal apertures which appear black. Pigment is absent from the margins of the colony, which are cream. White spicules are crowded into the branchial siphons creating white spots on the surface, although when the apertures are open in life the chinese orange[R] zooids are seen. In preservative the upper surface is black, the zooids are brown and diffused yellowish-brown pigment

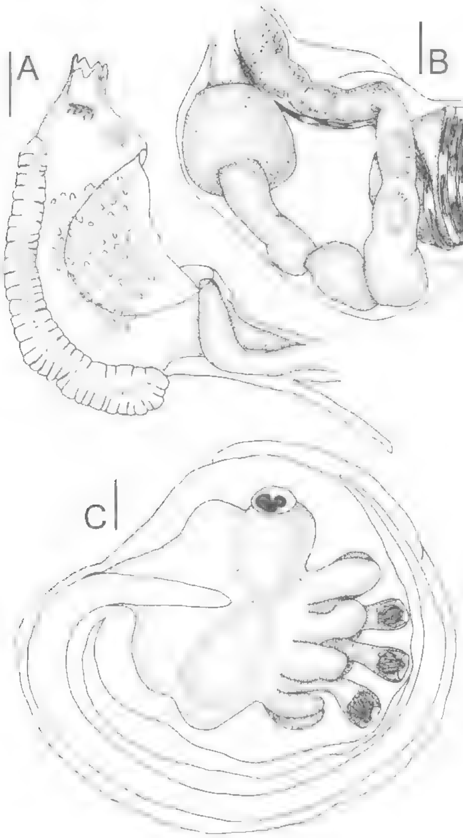


FIG. 102. *Didemnum oblitum* sp. nov. (QM G308386) – A, thorax; B, gut loop and testis; D, larva. Scales: 0.1mm.

is in the basal test and amongst the spicules in the outer margins of the colonies. Reservoirs of black pigment also are in the basal test. The preservative stains brownish yellow.

Colonies are very soft, despite the spicules being crowded throughout. A large horizontal cloacal cavity is at thorax level with thoraces crossing it independently in their own test sheaths. The abdomina are embedded in the basal test, as are developing embryos.

Spicules are globular, rarely to 0.05mm in diameter and more often less than 0.04mm. Rays are compacted or separated but always are flat-tipped. They usually are thick and not particularly numerous, about 9–11 in optical transverse section.

ZOOIDS. The contracted zooids are about 1mm long. The thorax is small with only about 6 stigmata per row. A short but robust retractor projects from halfway down the short oesophageal neck. The post pyloric part of the gut loop is bent up against proximal part. The vas deferens is coiled 8 times around the undivided testis. In preservative, brown embryos are being incubated in the basal test of the holotype colony. The larval trunk is 0.75mm long, the tail is wound about two-thirds of the way around it. Four ectodermal ampullae are along each side of the 3 antero-median adhesive organs, and an otolith and an ocellus are present.

REMARKS. The colonies resemble those of *Lissoclinum badium* with their slate grey colour with spicules crowded in the sides and base (which are white as a result). Both species have vast cloacal cavities, and are soft and thin. However, in *L. badium*, the surface test has yellow pigment mixed with the black, the cloacal cavity is deeper (extending the full length of the zooid), and the colony is more rubbery. Zooids of *L. badium* are not chinese[R]- or orpiment-orange[R] in life as are those of the present species. The globular spicules are larger and have fewer rays than those of *D. albopunctatum* or *D. fragile*.

D. brevioris Monniot, F. & Monniot, C., 1997 from Tanzania has spicules very like those of *D. oblitum*, and possibly the same size (although the maximum size of *D. brevioris* spicules is not recorded). In both species the zooids remain brown in preservative, although *D. brevioris* lacks the black pigment that is in the surface test of the present species, and it has a smaller larva with a blastozooid. Larvae of the present species are characteristic of *Didemnum*, with 4 pairs of ectodermal ampullae and they have no characters that would distinguish them from other species.

Didemnum ossium sp. nov.
(Figs 103, 168C; Pl. 12C;D)

Didemnum (Didemnum) misakiense: Tokioka, 1967: 75 (part, specimens from the Philippines).
Didemnum spongioides: Millar, 1975: 232.
Didemnum ligulum: Monniot, 1995: 313.

TYPE LOCALITY. Western Australia (Fenelon I., Institut Is, Bonaparte Archipelago 14°08.3S 125°41.5E, 20m dead coral, rock substrate with gorgonians and sponges, coll. AIMS Bioactivity Group 19.8.91, holotype QM G300986; Monte Bello Is 8ml NW Flag 1. 20°27.08S 115°30.09'E, sandy slope 4m, coll. AIMS Bioactivity Group 27.8.88, paratype QM G302927; Lord Mayor Shoal 20m, coll AIMS Bioactivity Group 13.8.91, paratype QM G300967).

FURTHER RECORD: Northern Territory (English Company Is, QM G302908).

PREVIOUSLY RECORDED. Western Pacific (New Caledonia – Monniot, 1995; Philippines – Tokioka, 1967; Millar, 1975).

The species is said to be rare in all newly recorded locations.

COLONY. In life colonies are sessile hemispherical clumps of relatively fleshy yellowish cream to yellow, or orange and red, or red, club-shaped to cylindrical and often branched lobes about 3cm diameter with randomly distributed and terminal common cloacal apertures. In preservative, there are stalk like branches only about 1.5cm diameter as well as wider and flattened lamellae which look like white curved bones. A posterior abdominal common cloacal cavity separates the outer zooid layer from a core of test and is continuous with thoracic spaces that penetrate in amongst the thoraces. Spicules are particularly crowded in the very centre and form a hard rigid rod in the cylindrical lobes and 2 or 3 parallel rods extending down the central test of the lamellae. Spicules are slightly less crowded in the remainder of the test. Large elliptical openings randomly placed over the surface are from depressions harbouring commensal amphipods. The connecting strands of test between the surface zooid-bearing layer, and the central core of test are relatively few.

Spicules of 2 types, stellate to 0.06mm diameter with 11–13 long, sharply pointed conical rays in optical transverse section, sometimes with bifid tips; or smaller more mulberry-like to globular spicules with short rounded or flat-tipped rays. Generally rays of the stellate spicules are not very crowded and seem isolated from one another on the central mass and often there are what appear to be stumps of broken rays amongst the others.

ZOOIDS. Zooids are robust. A relatively long cylindrical or tulip-shaped branchial siphon with 6 points around the aperture is about the same length as the contracted thorax. A bifid atrial tongue of varying size protrudes from the anterior rim of the aperture. A large oval lateral organ is on each side of the thorax.

Ten stigmata were detected in the anterior row of the branchial sac. A long tapering retractor muscle extends from about halfway down the oesophagus through the whole thickness of the zooid layer of the test. The post-pyloric part of the gut loop bends up to form a double loop. The testis is top-shaped, coming to a distinct point at the proximal end of the vas deferens which coils 9 times around it.

Embryos and larvae are present in all newly recorded (collected in August and November)

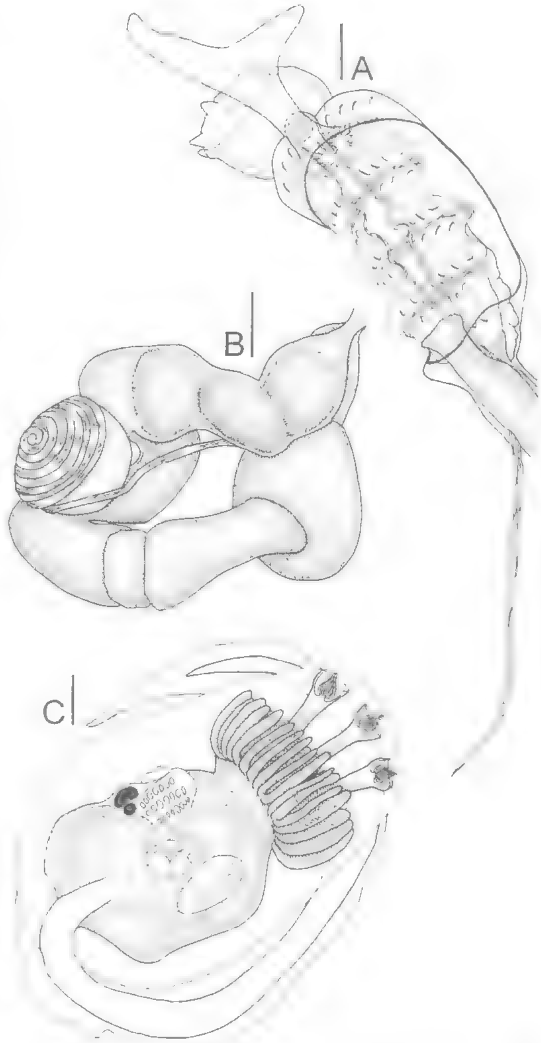


FIG. 103. *Didemnum ossium* sp. nov. (A, QM G302927; B,C, QM G300986) – A, thorax from dorsal surface; B, gut loop and testis; C, larva. Scales: 0.1mm.

and previously recorded colonies except one from the Philippines (Tokioka, 1967). The larval trunk is 0.9mm long and the tail is wound two-thirds of the way around it. A distinctive corolla of 34 long narrow, blade-like ectodermal ampullae encircle the anterior end of the larval trunk with its 3 antero-median stalked adhesive organs. The axial cones of the adhesive organs are turnip-shaped. A slight waist separates the adhesive array at the anterior end of the trunk from the developing oozooid and blastozooids in the posterior two-thirds of the trunk. The larval pharynx has about 9 stigmata in the first row of 3,

and the thoracic blastozooid (at the base of the oesophageal neck on the right side of the trunk) also has 9 stigmata per row. Halfway up the oesophageal neck on the same side is an abdominal blastozooid. An otolith and an ocellus are in the cerebral vesicle.

REMARKS. Although the colour of living specimens is variable the species always has characteristic lobed colonies, posterior abdominal common cloacal cavities, 2 types of spicules (one with blunt-tipped rays and others with sharply pointed and numerous rays), a conspicuous branchial siphon, small atrial lip, and an unusual larva with a corolla of numerous narrow ectodermal ampullae and blastozooids.

Temperate *D. lissoclinum* has similar colonies, but different spicules, zooids and larvae. *D. inveteratum*, known only from NW Australia where it occurs within the range of the present species, has similar but larger spicules, and a thin, hard, encrusting colony without posterior abdominal cloacal cavities. Spicules of the present species are similar to, but smaller with more rays and are more crowded than in *D. elongatum*. Also, *D. elongatum* has a different colony form, longer branchial siphon and oesophageal neck, and only 6 coils of the vas deferens. The colony of the present species slightly resembles that of *D. spongioide*, but the lobes do not anastomose in the same way, the surface is smooth, spicules have more numerous and more acutely pointed rays, the surface layer of test over the thoracic component of the cloacal cavities is thicker, branchial siphons longer, and larvae have more ectodermal ampullae.

Japanese *D. misakiense* (Oka & Willey, 1892), to which Tokioka (1967) had assigned Philippine colonies of the present species, has smaller spicules with fewer rays. Larvae of the Japanese species are not yet known. Species known to have a similar larva (with 30 ectodermal ampullae and blastozooids) are few, viz. *D. ligulum* Monniot, 1983 from Guadaloupe (with large spicules and 19 or more robust conical rays: see *D. arancium*, Remarks). *D. linguiferum* Monniot & Monniot, 1996 from Indonesia (with thoracic common cloacal cavities, not more than 6 stigmata in a row, only about 6 coils of the vas deferens, and large spicules to 0.08mm diameter with 15–17 robust conical rays), and *D. guttatum* Monniot & Monniot, 1996 from Indonesia (with relatively few spicule rays, rounded ectodermal ampullae and thoracic cloacal cavities).

D. ligulum: Monniot, 1995 from New Caledonia has an identical colony (Monniot et al., 1991: 179, not Monniot & Monniot, 1981 (sic) as cited in Monniot, 1995: fig. 8 caption) to the type material of the present species and to previously recorded synonyms (Tokioka, 1967; Millar, 1975). Zooids and larvae (where present) are also similar except for the usual variations in the reported numbers of stigmata and coils of the vas deferens. The rounded or flat-tipped spicules are not recorded for the synonyms listed above, maximum spicule size and diversity have not been reported. Monniot & Monniot (1996, pl. 2C) had an opportunity to examine the spicules by SEM, and illustrated only stellate spicules. These are identical with the types, as are all other characters. Further examination could demonstrate the same diversity in the spicules as in the type material .

Didemnum parancium sp. nov.
(Figs 104, 166E)

TYPE LOCALITY. Queensland (Bowden Reef off Townsville, 190°3.1S 147°55.6E coral reef crevices, caves 10m, coll. AIMS Bioactivity Group 6.2.87, holotype QM GH5353).

COLONY. The colony is a smooth, thin (about 2mm) encrusting sheet, crowded with spicules and with a rippled base. Living, it is pink/orange. Despite the crowded spicules, and possibly because they are so small, the colony is flexible. Branchial apertures are apparent from the surface as small beige dimples arranged more or less in double circles. However, neither common cloacal canals nor common cloacal apertures were detected. Although mature larvae are being incubated in the basal test and sperm are present in mature testes and vasa deferentia, the colony is in vegetative phase with thoracic buds in the oesophageal region. Zooids occupy the full depth of the colony and larvae are embedded in the base.

Spicules are small (to 0.04mm diameter) globular and burr-like with numerous long rod-like rays.

ZOOIDS. Thoraces are relatively long and narrow with a short branchial siphon. A short, narrow retractor muscle projects from the top of the oesophageal neck. Eight stigmata are in the 2 anterior rows, reducing to 6 in the posterior rows.

The gut forms a rounded loop, curved ventrally with the testis against the postero-dorsal side of the distal part of the loop to form a rounded, almost spherical, abdomen. The vas deferens

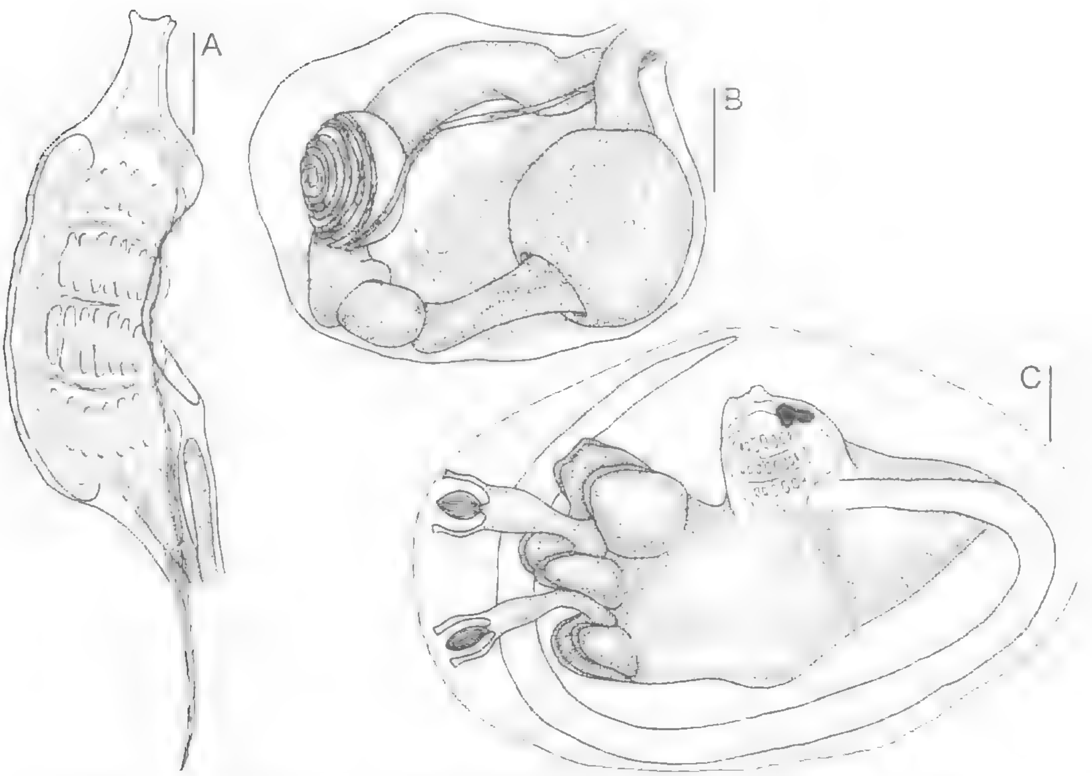


FIG. 104. *Didemnum parancium* sp. nov. (QM G 5353) – A, thorax; B, gut loop and testis; C, larva. Scales: 0.1mm.

makes 6 coils around the outer shallow dome-like surface of the undivided testis. Conspicuous spherical translucent cells, 0.01mm in diameter, are in the haemocoel beneath the epidermis of the zooid and are especially crowded around the gut loop, between the 2 limbs of the loop and in the major blood sinuses.

The larval trunk is 0.8mm long and the tail is wound three-quarters of the way around it. Three pairs of ectodermal ampullae and 2 antero-median adhesive organs were in 3 of the 4 examined larvae, but the other larva had 3 adhesive organs. The spherical cells present in the haemocoel of the adult zooids are also present in the posterior end of the larval haemocoel behind the oozooid. A mass of yolk is present anterior to it.

REMARKS. The spicules resemble those of *D. fragile* and *D. albopunctatum*, but they have a greater maximum diameter. The former species is a similar colour (pink/orange) and has a similar number of vas deferens coils, but it has 4 pairs of ectodermal ampullae and always 3 adhesive organs. The latter has only 2 adhesive organs but it has 4 pairs of ectodermal ampullae more numerous coils of the vas deferens, the colony has dark pigment in the surface and a conspicuous superficial bladder cell layer. *D. pitipiri* Monniot & Monniot, 1987, from French Polynesia, also has only 2 adhesive organs but 6 pairs of epidermal ampullae, and stellate spicules with conical rays. *D. parau* Monniot & Monniot, 1987 has similar but smaller spicules, 6 vas deferens coils, and a similar-sized larval trunk, but it has 3 adhesive organs and 4 pairs of lateral ampullae. *D. parancium* is characterised by its burr-like spicules, 2 or 3 adhesive organs, 3 pairs of ectodermal ampullae, 6 coils of the vas deferens and a thin colony. The large brown spherical cells in the adult and larval haemocoel occur in other species (see Glossary, **haemocoel**).

Didemnum patulum (Herdman, 1899)
(Figs 105A,B, 169-I; Pl.12E)

Leptoclinum patulum Herdman, 1898: 448 (nom. nud.); 1899: 92. Herdman & Riddell, 1913: 888.

Not *Didemnum patulum*: Kott, 1972a: 18; 1972b: 179; 1976: 65; 1998: 83 (< *D. macrosiphonium*).

Didemnum augusti: Kott, 1962: 323 (part, colony from Balnarring Beach); 1998: 81 (part, Balnarring Beach only).

NEW RECORDS. Victoria (Gabo I., SAM E2839; Cape Woolamai, MVF70223; Western Port, QM G302899; Bass Strait, MVF70207).

PREVIOUSLY RECORDED. Victoria (Balnarring Beach – Kott, 1962). New South Wales (Port Jackson – Herdman 1899).

COLONY. The newly recorded colonies are thin, hard, investing sheets about 5mm thick growing around sponge or weeds. Zooids are along each side of the deep but narrow canals that surround slightly elevated, oval, opaque, paler zooid-free areas, about 2–3mm in maximum extent, that form a mosaic on the upper surface. The surface of the preserved colony is slightly depressed over the cloacal canals, and the test is slightly translucent, owing to the relatively shallow depth of spicules in the layer over the canals contrasting with the opaque zooid-free areas which extend through the whole thickness of the colony. Sessile common cloacal apertures occur randomly at junctions of the cloacal canals. Spicules are present throughout and continue without interruption down into the siphon linings. They are slightly less crowded in the lower half than in the upper part of the colony, although a crowded layer is on the base. They are stellate, to 0.07mm in diameter, with 9–11 relatively short, blunt conical rays in optical transverse section. Ray length/spicule diameter ratio is about 0.24.

ZOOIDS. Zooids are not readily removed from the test, possibly owing to the crowded spicules, and were examined in stained, decalcified slices of the colony. They are particularly small, the contracted thorax being about 0.2mm long, and are covered with distinct projecting, round-tipped, columnar epidermal cells. The branchial siphon is short, with 6 narrow pointed lobes around its rim. A strong, tapering retractor muscle projects out from halfway down the long oesophageal neck. The atrial aperture is sessile, exposing a large part of the branchial sac directly to the cloacal canal. Gonads are not developed in the newly recorded zooids, nor are they described for the holotype. Kott (1962) recorded 8 coils of the vas deferens around an undivided testis in the specimens from Balnarring Beach.

REMARKS. The holotype is a large colony (8cm maximum dimension). The mesh-work of grey lines is present in both the type and one of the newly recorded specimens (QM G302899), although the other (SAM E2839) has more crowded spicules than those reported by Herdman (1899) and there is no trace of pigment.

The specimen of *D. augusti*: Kott, 1962 was assigned on the basis of the cloacal systems. This type of cloacal system with zooids along each side of canals that surround spicule-free areas does occur in other species in this genus (e.g. *D. microthoracicum*, *D. macrosiphonium*). As Kott (1962) pointed out, *D. augusti* Michaelsen from the western Indian Ocean differs from the Australian specimens (which she had thought to be conspecific) in its spicules. It is clearly a different species. The specimen of *D. augusti*: Kott, 1962 from Balnarring Beach belongs to the present species; colonies from Reevesby I. probably are *D. microthoracicum*; and those from Western Australia with 2 testis follicles belong to a third (as yet undetermined) species. *D. patulum*: Kott, 1972a,b and 1976, respectively from South Australia and Port Phillip Bay (Victoria), with similar cloacal systems, but larger zooids, longer branchial siphons and an atrial tongue from the body wall anterior to the rim of each opening, belong to *D. macrosiphonium*. *D. crescente*, a sympatric species, has similar cloacal systems but spicules with fewer and longer rays.

Didemnum pecten sp. nov.
(Figs 105C–F, 170A; Pl. 12F–H)

TYPE LOCALITY. South Australia (Kangaroo I., 35°45.9 S, 137° 46.5' E, underside of overhang 6m, strong current, coll. AIMS Bioactivity Group 1.2.89, holotype QM G300929).

FURTHER RECORDS. South Australia (Point Souttar, QM GH5439). Victoria (Lorne, AM Y2319). New South Wales (Jervis Bay, QM G302898).

COLONY. The holotype colony consists of double-sided fan-shaped, branching lamellae, probably standing vertically, with the upper margin and one side of the lamella produced into rounded, stumpy lobes, each with a terminal common cloacal aperture. The colony from Lorne (AM Y2319) is similar — an extensive but irregular sheet with small cylindrical elevations crowded at one end, each with a terminal common cloacal aperture. The colony from Jervis Bay is a clump of rounded upright lobes joined basally, each tapering to a terminal common cloacal aperture. The test is firm, the outer surface smooth with a thin superficial layer of bladder cells over a layer of spicules at branchial siphon level. Spicules are absent from the remainder of the colony. Thoracic common cloacal canals penetrate between the zooids which are crowded in a layer beneath the spicules. The zooid layer of the colony is

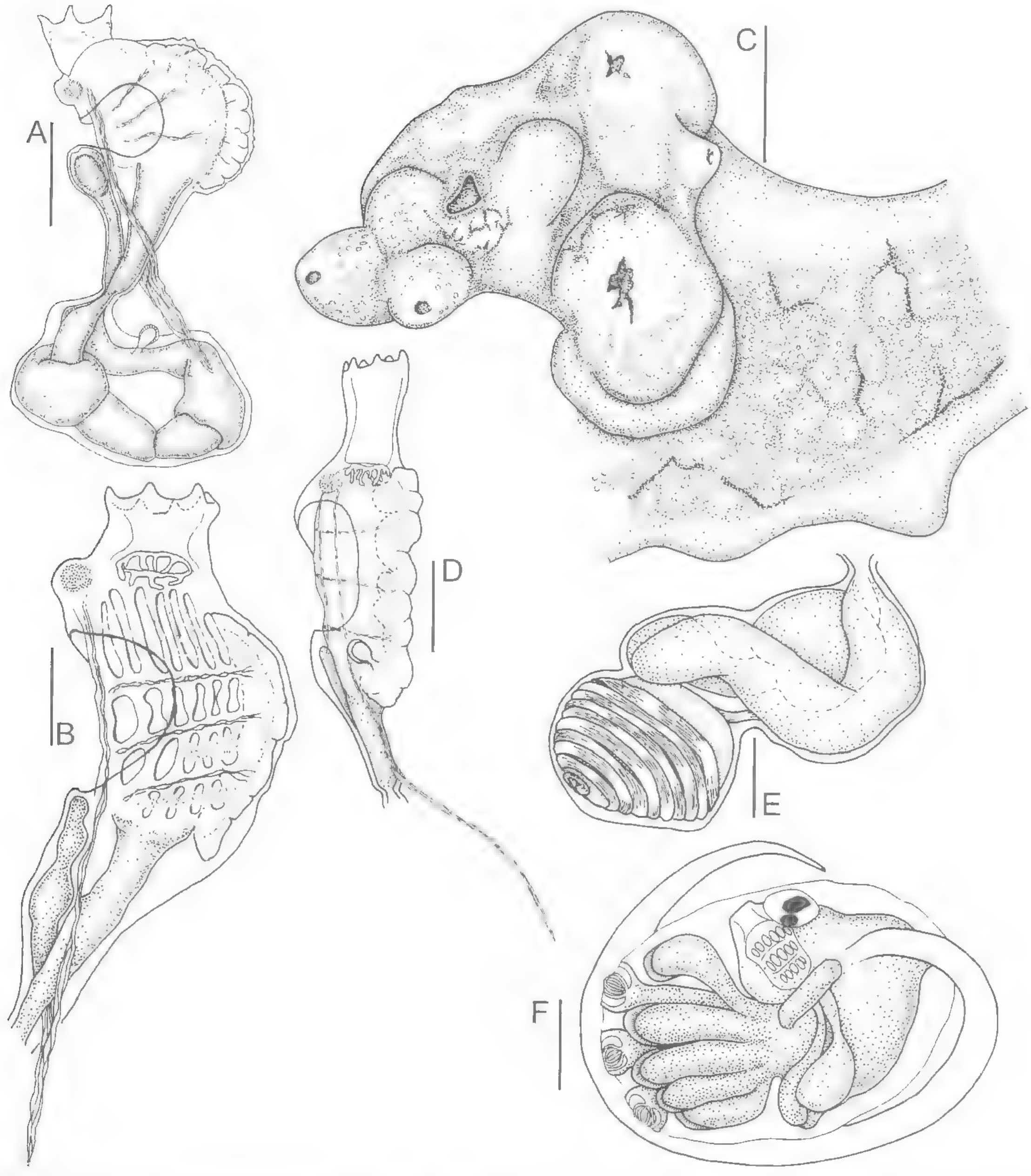


FIG. 105. A, B, *Didemnum patulum* (A, SAM E2839; B, MV F70207) – A, zooid; B, thorax. C–F, *Didemnum pecten* sp. nov. (C, AMY2319; D,F, QM G300929; E, QM G302898) – C, portion of colony; D, thorax; E, gut loop and testis; F, larva. Scales: A,B,D–F, 0.1mm; C, 1.0cm.

separated from a central core of text by extensive posterior abdominal common cloacal spaces. The spicules are up to 0.065mm diameter, although smaller ones predominate. They are stellate, with 9–11 and occasionally only 7 conical rays in optical transverse section but the conical rays are broadly based rather than slender and are blunt-tipped. The ray length/spicule diameter ratio is about 0.36.

In life the colonies are bright red-orange. They are common in otherwise predominantly sponge communities at known locations.

ZOOIDS. Branchial siphons are long, almost half the length of the thorax, with 6 narrow points around the opening. Generally the thorax is roughly rectangular, with much of the branchial sac exposed directly to the common cloacal cavity by the wide open atrial aperture. Only about 6 stigmata are in each row, but these could not be counted accurately. The thorax (excluding the branchial siphon), oesophageal neck and post-oesophageal part of the gut loop are all about one-third of the length of the zooid, which is only about 1mm overall. A retractor muscle projects from about halfway down the oesophageal neck. The markedly dome-shaped testes at the side of the post-pyloric part of the gut loop has 9 coils of the vas deferens around it. Larvae, present in the holotype and the colony from Lorne (AM Y2319), collected in November, are in the central test, the larval trunk is about 0.5mm long and the tail is wound all the way around it. Five long, finger-like ectodermal ampullae are along each side of the 3 antero-median adhesive organs.

REMARKS. The species resembles the tropical *D. roberti* which also has vertical lamellae strengthened by a firm central test core surrounded by posterior abdominal common cloacal cavities, a similar small larva (but with only 4 lateral ampullae per side) and spicules principally in a layer beneath the surface. However, *D. roberti* has larger spicules (to 0.09mm diameter) with attenuated rays. *D. sucosum* resembles the present species in colony form and cloacal systems but has larger spicules (to 0.125mm diameter)

D.fragum is a sympatric species with long branchial siphons, similar but larger zooids, more vase-shaped single to 3-lobed colonies, larger spicules with more and shorter rays, more (12) coils of the vas deferens and a larger larva with more (6 per side) larval lateral ampullae. *D. pellucidum* also has a larger larval trunk, and more (12 per side) larval lateral ampullae and larger spicules (to 0.1mm diameter). The temperate *D. spadix* has similar spicules, but its thin, sheet-like colony with spicules crowded throughout, absence of a posterior abdominal cloacal cavity and free spherical brown cells in the colony distinguish it from the present species.

Didemnum pellucidum sp. nov.
(Figs 106, 169C; Pl. 13A–C)

TYPE LOCALITY. South Australia (Yorke Peninsula. Edithburgh jetty pile with *Botrylloides leachi*, 2 to 3m, coll. K.L. Gowlett Holmes 11.4.92, holotype SAM E2622). Western Australia (South of Yallingup, canal rocks off boat ramp under limestone ledge 2m, coll. K.L. Gowlett Holmes 19.1.93, paratype SAM E2696; Rottnest I., off Parker Point, rocky reef, high energy location 9 m on wall beneath undercut, coll. AIMS Bioactivity Group, 15.3.89, paratype QM G300985).

FURTHER RECORDS. South Australia (Yorke Peninsula, QM G300944; Eyre Peninsula, SAM E2651; St Vincent Gulf, SAM E2606, E2654-5; Kangaroo I., SAM E2858).

COLONY. The colonies form soft, bulky, fleshy, but robust often irregular masses, with rounded margins, almost cylindrical branches, dome-like swellings (about 1cm in diameter) and rounded ridges. One colony (QM G300944) is a number of vertical lamellae that branch and fuse and separate into dome-shaped lobes or ridges on the upper surface. Another (SAM E2606) is a massive hemisphere composed of vertical lobes that fuse along their length but separate out into dome-shaped prominences or ridges with terminal common cloacal apertures on the upper surface. The surface of all colonies is smooth but sometimes creased. Common cloacal apertures are terminal on the vertical lobes and around the rounded margin of the colony. Zooids are in groups in the upper part of the fleshy colonies. The common cloacal cavity is deep around each group of zooids, extending into a vast posterior abdominal cloacal cavity which is interrupted by relatively few narrow vertical connectives joining surface zooid-containing layers to the basal or central test. The cavity also penetrates each group of zooids at thorax level. On the surface of the colony, the branchial apertures sometimes are drawn down into the soft thick upper layer of test. They are conspicuous as white spots created by the plug of crowded spicules in the siphon linings. The branchial siphons are long, about half length of thorax or more (to extend through the upper layer of test), and often tear when attempts are made to remove zooids from the test.

Generally, sparse, but evenly spaced spicules are in the surface of the colony and around the zooids. They are slightly more crowded over the top of the branchial siphons and down into the siphonal linings than they are between the zooids (although this could result from contraction of the zooids) and they are present in a thin layer on the base of the colony but are sparse or absent from the remainder of the test. However, in one of the paratypes (QM G300985) spicules are moderately crowded throughout the test. Spicules have a big size range, smaller ones and larger ones (occasionally to 0.1mm diameter)

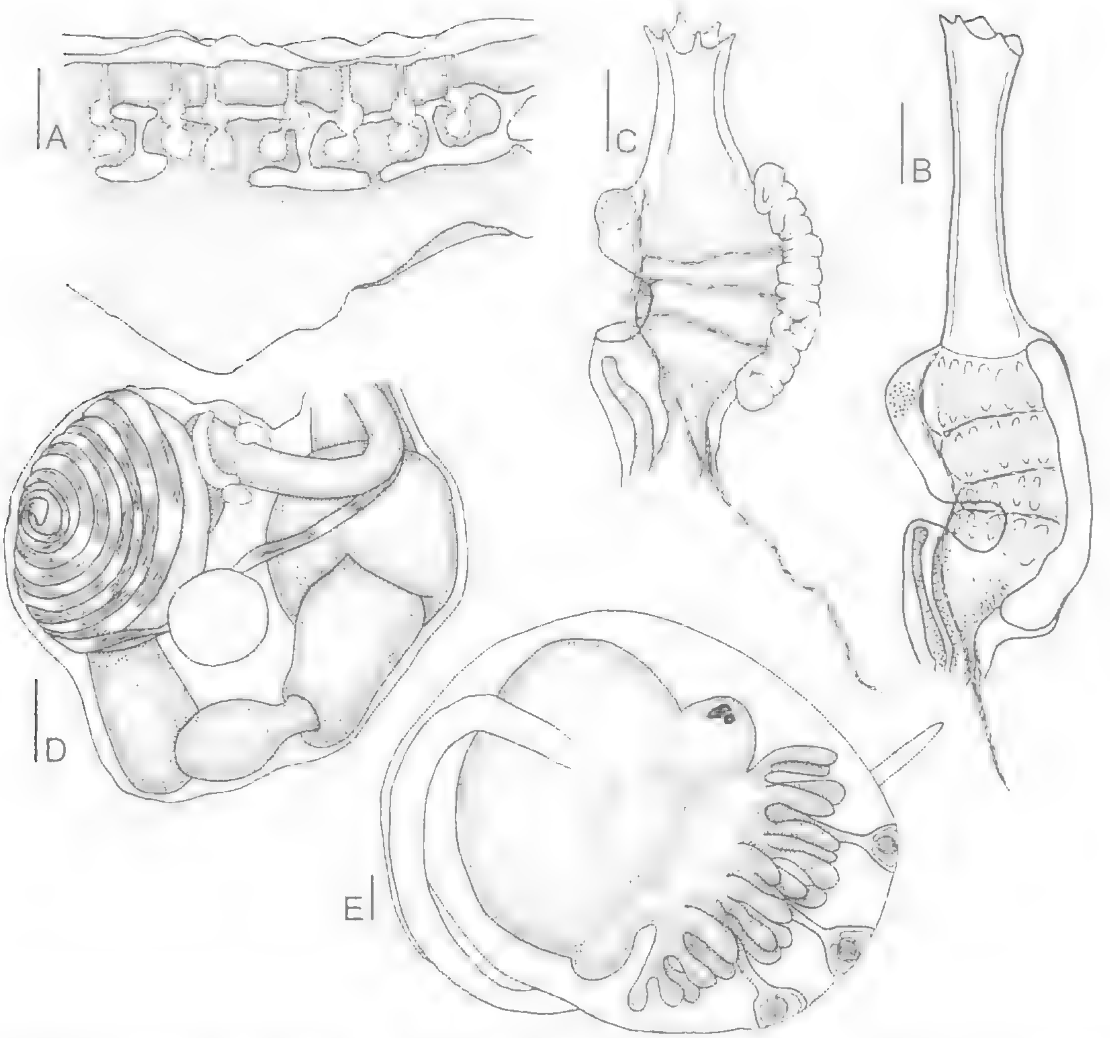


FIG. 106. *Didemnum pellucidum* sp. nov. (A,E, SAM E2696; B, QM G300985; C,D, SAM E2622) – A, vertical section of colony; B,C, thoraces; D, gut loop and gonads; E, larva. Scales: A, 1.0mm; B-E, 0.1mm.

being present in more or less similar numbers. They have 7–11 moderately long conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.3.

Most colonies were bright red to pink in life.

ZOOIDS. Zooids are relatively small being about 1.5mm long, including the long cylindrical branchial siphon which sometimes (SAM E2654) is up to 3 times the length of the body and is never less than half the length of the thorax. Conspicuous projecting columnar epithelial cells on the thorax may contribute to the tight hold that the test has on the zooids. Six short, sharply pointed lobes are on the rim of the branchial aperture. The atrial aperture is simple and sessile. A small lateral organ is on each side of the thorax. A retractor muscle projects out into the test from about halfway down the oesophageal neck. The distal part of the gut loop is flexed ventrally. Testes are mature in the holotype and in the specimen from the Eyre Peninsular (SAM E2651) collected in February. The testis is undivided, and is surrounded by 9 close coils of the vas deferens.

Almost spherical, large larvae are in the paratype (SAM E2696). The trunk is 1.2mm long with the short tail wound barely halfway around it. Twelve or more long, club-shaped ectodermal ampullae are along each side of the 3 antero-median adhesive organs. As the larvae

mature the number of ectodermal ampulla appears to increase by division and also by additional ones developing from the prolongation of the frontal plate ventrally. A large, projecting horizontal lateral ampulla extends back from the neck region on the left side of the larval trunk. The oozooid in the centre of the trunk has 3 rows of stigmata and a long narrow, vertical gut loop stretched through the thickest part of the larval trunk. Blastozooids are not present.

REMARKS. The species is characterised by its lobed, fleshy often complex colonies with terminal cloacal apertures, thick surface layer of test, long branchial siphons, extensive horizontal posterior abdominal cloacal cavity and numerous vas deferens coils. The large larva, without blastozooids and with a relatively large number of lateral ampullae also is unusual.

Other lobed colonies from southern Australia with terminal common cloacal apertures are *D. fragum*, *D. pecten* and *D. sucosum*. The colony of *D. fragum* is 1–3 lobed, has smaller spicules and fewer (6) larval ectodermal ampullae per side; *D. pecten* has numerous lobes that do not fuse with one another as they do in the present species, and its larvae are smaller with only 5 lateral ampullae per side. *D. sucosum* has larger spicules with more rays than the present species.

Although *D. cygnuus*, *D. elongatum*, *D. macrosiphonium* and *D. guttatum* all have long branchial siphons they are not longer than the thorax, as they sometimes are in the present species. Further, *D. macrosiphonium* has larger zooids, and smaller spicules which like *D. elongatum*, are of 2 different sorts. *D. cygnuus* and *D. guttatum* have fewer spicule rays. *D. patulum* resembles the present species in its spicules (some larger ones having fewer rays than others) and their distribution (becoming sparse in the basal test). However the spicules of *D. patulum* generally are smaller, it lacks a long branchial siphon and its grey beige pigmentation forming a network in the surface further distinguishes it. *D. lissoclinum* has similar colonies but lacks the long branchial siphon and has spicules crowded throughout.

Tropical *D. caesium* has similar spicules of comparable size and it has fleshy colonies. However its single layer of spicules is beneath a conspicuous bladder cell layer, its dark pigment persists in preservative, its large zooids do not have the long branchial siphons of the present species and it has long, bifid, atrial lips.

Leptoclinides comitus from Port Davey has similar, fleshy colonies with spicules in a surface layer and few elsewhere. It is distinguished from the present species primarily by its generic characters, and by its globular spicules (rather than large stellate ones).

Didemnum perplexum sp. nov.
(Figs 107, 170F; Pl. 13D–F)

Didemnum makropnous Sluiter, 1909: 56 (part, ZMA TU461.2. statn 99).
Didemnum albopunctatum Sluiter, 1909: 58 (part, ZMA TU433.1 statn 273).
Didemnum jedanense Sluiter, 1909: 58 (part, ZMA TU454.2 statn 273).
Didemnum rodriguesi Rocha & Monniot, 1993: 261 (part, specimens from New Caledonia).
? *Didemnum granulatum*: Rocha & Monniot, 1993: 261.

TYPE LOCALITY. Queensland (filter of sea water intake, Heron I. Research Station, coll. P. Kott et al., 5.3.93, holotype QM G308117; Wistari Reef Capricorn Group 15m, coll. P. Kott et al., 11.3.93, paratype QM G302960; eastern end Heron I. reef, coll P. Kott 9.3.93, paratype QM G308046).

FURTHER RECORDS. Queensland (Heron I., QM G308033, G308208, G308212, G308228-9; Swain Reefs, QM G305622, G305751, G305796-7, G305803, G305807, G305649, G305698-9, G308398).

PREVIOUSLY RECORDED. New Caledonia (Rocha & Monniot, 1993). Indonesia (ZMA TU433.1, TU454.2, TU461.2 Sluiter, 1909).

COLONY. Colonies usually form thin, hard encrusting sheets (on the undersides of boulders) that break up readily. Many specimens have minute spicule-filled papillae crowded on the otherwise smooth surface of some parts or all of the colony. There is not a superficial bladder cell layer. Minute dark spherical pigment cells are in the test mixed with spicules. Pigment distribution is interrupted by short, narrow lines of white spicules that create the reticular pattern often seen on the surface of the colony. The dark vermilion pigment is especially crowded around the rim of the common cloacal apertures, where the spicules are missing. The zooids also are strongly pigmented and can be seen through the surface test where the spicules are less crowded over the zooids. Spicules continue down into the lining of the branchial siphons and seen from the surface a margin of spicules usually lines the stellate branchial apertures. Spicules are crowded throughout the colony, which is hard and brittle. Living colonies are coral red[R], orange chrome[R], orpiment orange[R], scarlet[R]- or orange-vermilion[R], flame scarlet[R] or vermilion[R]. Dark spots occur where the dark orange, scarlet[R] to claret brown[R], or burnt carmine[R] zooids show

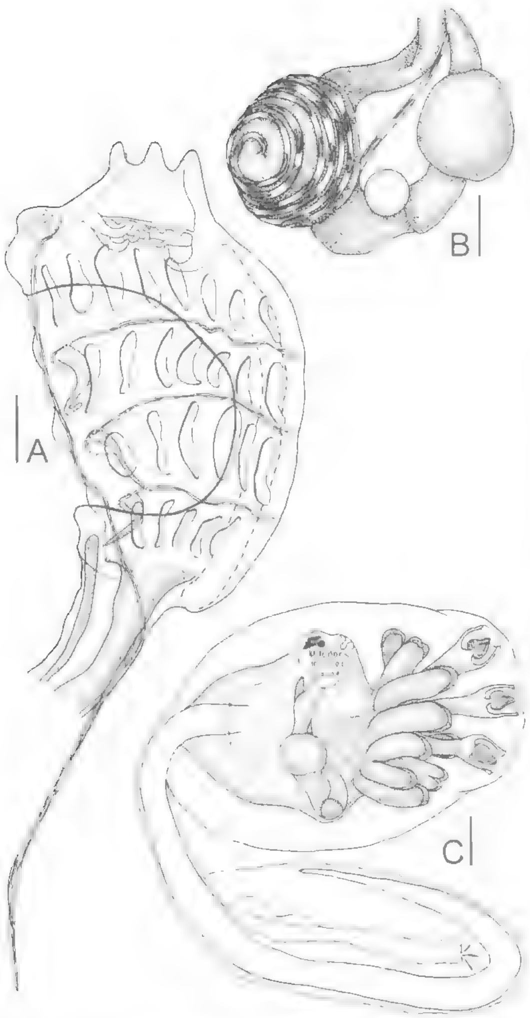


FIG. 107. *Didemnum perplexum* sp. nov. (A,B, QM G308046; C, QM G308117) – A, thorax; B, gut loop and gonads; C, larva. Scales: 0.1mm.

through the branchial apertures causing the colonies to be described as 'spotted.' The common cloacal cavity is thoracic, but it varies in depth, sometimes being shallow with the zooids largely embedded in the test, while in other specimens it is deeper, the thoraces and sometimes the whole zooid being suspended between surface and basal layers of test across the cloacal cavity in its own test sheath.

Spicules are up to 0.06mm diameter with 5–7 and sometimes 9 rays in optical transverse section. They sometimes have blunt-tipped and occasionally almost rod-like rays, but most often the rays, although quite long with a ray length/spicule diameter ratio to 0.4, are conical and pointed.

In preservative the colonies are brownish-yellow on the surface, and cream internally with yellowish or orange or brownish-orange zooids. Darker tones of orange are in the buds and endostyle, and eggs also are dark-orange. The preservative is stained a lemon-orange to yellowish-brown urine colour and labels often are stained.

ZOOIDS. Zooids are relatively robust, especially the abdomen. The thorax is turnip-shaped, a moderately long branchial siphon has 6 shallow lobes around the aperture and the atrial aperture is wide and open, exposing much of the branchial sac directly to the cloacal cavity. In the branchial sac, 8 stigmata are in the anterior row, the second row contains 7 stigmata, the third 6, and the fourth row has 5. The retractor muscle is thin and is free of the zooid from about halfway down a relatively long oesophageal neck. The gut loop is open, the whole loop curved up horizontally, but also the pyloric part of the loop is bent ventrally to form a double loop. The duodenum is long and inflated at its distal end, the posterior stomach is small, and the rectum long and narrow. The gonads lie against the ventrally flexed post-pyloric part of the gut loop. The testis is dome-shaped with 7 coils of the vas deferens around its outer surface.

Larvae are present in the surface test of colonies collected from Heron I. (QM G308046, G308117) in March and from the Swain Reefs (QM G305803, G305807) in July. They appear to be liberated through the surface of the colony. They also are known from the New Caledonian material (Rocha & Monniot, 1993). They have a trunk 0.6–0.88mm long, 6 pairs of lateral ampullae — 12 in all, arranged in a circle around the 3 adhesive organs and a tail that curves about two-thirds of the way around the trunk.

REMARKS. The Brazilian *D. rodriguesi* Rocha & Monniot, 1993, to which the New Caledonian specimens were assigned, differs from the present Pacific species in its smaller spicules. The largest spicules in *D. rodriguesi* are only half the diameter of the largest spicules in the present species.The reticulate appearance of the surface, which Rocha & Monniot (1993) believe is characteristic of *D. rodriguesi*, is seen in other species (*D. moseleyi*). It is more an optical illusion than a definite pattern, resulting from the crowded spicules sometimes appearing to be in short random rows. It occurs especially when

pigment is mixed with spicules rather than being crowded in a layer above the spicules. The absence of a posterior stomach is also an implied characteristic of the species Rocha and Monniot described. However, the definition of posterior pyloric sections of the gut is always subject to the condition of the gut when the organism was fixed. Similar variations in the condition of the gut loop are commonly encountered. Zooids with inflated gut in which the constrictions between the parts are not present, as well as narrower, less distended intestinal tubes are found in the newly recorded colonies. *D. granulatum* is distinguished from the present species (and from *D. rodriguesi*) by its smaller zooids, and 4 (rather than 6) pairs of larval lateral ampullae per side. Rocha & Monniot (1993) distinguished *D. rodriguesi* colonies from *D. granulatum* by the absence of spicule-filled papillae on the surface and the more intense colour of the colonies. Such papillae are variable in both species (and many others too) and the colour of the colonies is affected by their distribution on the surface. Neither colour nor the papillae are reliable distinguishing characters. The strong dorsal pharyngeal muscles are a family character.

D. granulatum lacks the intense opaque colour of the present species and has thicker, less brittle colonies and smaller zooids. *D. candidum* also has smaller spicules, most with rod-like rays. *D. captivum* Monniot, F. & Monniot, C., 1997 has similar spicules and zooids to the present species, but has more coils of the vas deferens and more larval lateral ampullae. *D. lacertosum* has different spicules altogether with longer rays. *D. membranaceum* has white spicules exposed around the numerous prominent common cloacal apertures, smaller zooids, more sharply pointed spicule rays and occasional spiky (sometimes giant) 4–6 rayed spicules. In *D. clavum* spicule rays are longer, rod-like, and it also has giant spiky spicules. *D. fuscum* has longer, more rod-like and more numerous spicule rays. *D. tonga*: Kott & Goodbody, 1981 has similar spicules, but with more rays and some giant spiky ones. It has 7 coils of the vas deferens, and pointed spicule-filled papillae on the surface but only 4 pairs of lateral larval ampullae. It is conspecific with *D. membranaceum*.

The species characteristics, evident in the newly recorded specimens and in those from Indonesia and New Caledonia are the spicules, with 5–7 and sometimes 9 conical rays, zooids with the post pyloric part of the gut bent up to form a double loop, 7 coils of the vas deferens (within the range 6 to 9 reported for the New Caledonian material), larvae with 6 ampullae per side, and darkly stained preservative.

Didemnum poecilomorpha
Monniot & Monniot, 1996
(Figs 108, 168B; Pl. 13G)

Didemnum poecilomorpha Monniot & Monniot, 1996: 160.
Didemnum viride: Kott, 1982a: 101.

NEW RECORDS. Western Australia (Broome, QM G308485). Papua New Guinea (Gazelle Peninsula, QM G302890).

PREVIOUSLY RECORDED. Western Pacific (Philippines – QM GH483, GH488 Kott, 1982a; Palau Is – QM GH498, GH501 Kott, 1982a; Monniot & Monniot, 1996; Indonesia – Monniot & Monniot, 1996).

COLONY. Colonies are tough, leathery, encrusting sheets with the surface marked into slightly elevated zooid-free longitudinal streaks and oval to circular opaque areas by slightly depressed translucent lines over narrow primary common cloacal canals that are lined on each side by zooid openings. The preservative is stained green and pools of blackish-green pigment and groups of green cells are in the basal test.

Spicules sometimes are relatively sparse in the superficial layer of test where they are mixed with bladder cells and plant cells. They are crowded at zooid level and throughout the remainder of these tough, solid colonies, although in one colony (QM G308485) the lower one-third (beneath the embedded abdomina) is transparent and spicule-free. The translucent lines over the common cloacal canals result from the lesser depth of spicule-containing test there than in the solid areas of test they surround. Spicules are of 2 types, stellate ones to 0.0625mm diameter with 11–13 pointed conical rays in optical transverse section and others with flat-tipped to rounded rays that are never as large as the stellate ones. The ray length/spicule diameter ratio of the stellate spicules is about 0.25.

ZOOIDS. Zooids are relatively small, to about 1.0mm long overall including a long branchial siphon sometimes almost as long as the thorax. Six sharp points are around the branchial aperture. The atrial aperture is a wide, rectangular opening around the branchial sac. The oesophageal neck is at least half, and the remainder of the abdomen is only about one-sixth of the total zooid length. The retractor muscle is particularly long and tapering, free of the oesophageal neck about two-thirds of the distance down it. The lateral organs are small

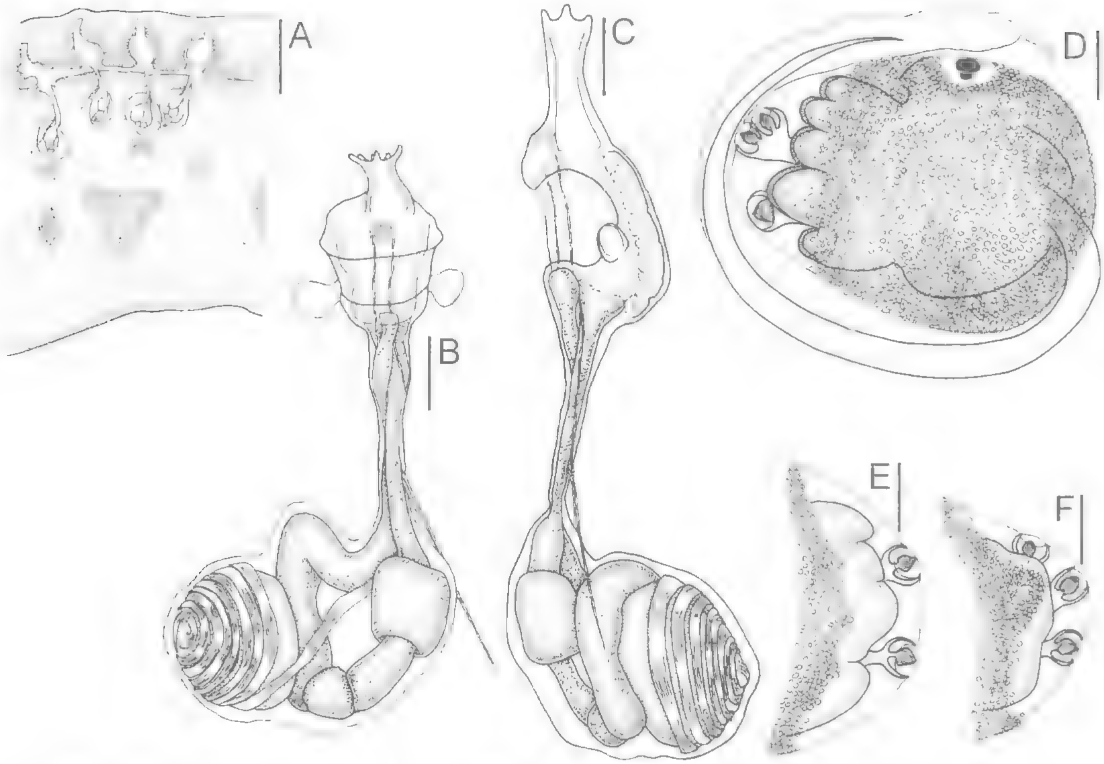


FIG. 108. *Didemnum poecilomorpha* (A,D–F, QM G302890; B,C, QM G308485) – A, vertical section through colony; B, zooid dorsal view; C, lateral view; D, larva with symbionts in larval test; E,F, anterior end of larvae showing variations in adhesive organs. Scales. A, 0.5mm; B–F, 0.1mm.

goblet-shaped projections from each side of the parietal thoracic wall opposite the last row of stigmata with their concavity directed ventrally. About 6 stigmata per row are in the branchial sac although these could not be counted exactly. The post-pyloric part of the gut makes a tight double loop in the distal tip of the abdomen. The conical to dome-shaped testis is behind the loop and 8 coils of the vas deferens surround it. A large spherical greenish-coloured egg is present in the abdomen of the western Australian specimens.

Embryos are developing in the basal test of the specimen from Papua New Guinea (collected in November). They move up toward the surface as they mature. The larval trunk is about 0.6mm long and is a deep, regular oval. The tail extends about two-thirds of the way around the trunk. Five rounded ectodermal ampullae are along each side of the antero-median adhesive organs. In 6 examined larvae, 3 have only 2 adhesive organs, 2 have the dorsal one partially subdivided and one has 3 separate adhesive organs as a result of the dorsal one subdividing. Nevertheless both Kott (1982a) and Monniot & Monniot (1996) found 3 larval adhesive organs. The larval test is filled with plant cells except for windows over the ocellus and otolith and in front of the adhesive organs.

REMARKS. The newly recorded specimens and the type material from Indonesia have similar colony form, arrangement of spicules, form and size of the stellate spicules, zooids, cloacaaal systems, similar sized larvae with 5 pairs of ectodermal ampullae and they all have plant cells embedded in the larval test leaving clear windows over the sensory and adhesive organs.

On re-examination, specimens from the Philippines and Palau Is, which Kott (1982a) assigned to *D. viride*, were found to contain globular as well as stellate spicules as in the newly recorded material. The globular spicules, which are patchy in their distribution, were not reported by Monniot & Monniot (1996).

The colonies, small zooids with long oesophageal neck, branchial siphon and 2 sorts of spicules do resemble *D. guttatum*, however the more numerous spicule rays, slightly larger

zooids and the more numerous larval ectodermal ampullae distinguish the present species.

Didemnum precocinum sp. nov.
(Figs 109, 165G; Pl. 13H)

?*Didemnum fragile* Sluiter, 1909: 56 (part, ZMA TU446.1A).
?*Didemnum candidum*: Hastings, 1931: 94 (part, pink shore specimens).

TYPE LOCALITY. Queensland (Wistari Reef, landing stage, low tide rubble fauna, coll. P. Kott 5.3.93, holotype QM G308026; Heron I. reef, eastern end, low tide rubble fauna, coll. P. Kott March 1993, paratype QM G308028).

FURTHER RECORDS. Western Australia (Ashmore Reef, WAM 521.92; Lesueur I. Kimberley, WAM 720.91). Queensland (Capricorn Group, QM G302977, G308156, G308496; Swain Reefs, QM G308368; ? Low Is – Hastings 1931). ? Indonesia (Sluiter, 1909).

COLONY. Colonies, never more than 2mm thick, are sometimes extensive sheets and always are flat and hard with large common cloacal apertures on randomly distributed shallow elevations of the surface. Some *Prochloron* is present on the surface. Spicules are crowded throughout, although sometimes there may be pigment cells scattered amongst them. In life, colonies are flesh coloured to whitish pink or orange, sometimes being described as orange spotted when the flame scarlet to cadmium orange zooids show through the branchial apertures. The common cloacal cavity is deep, the thoracic test sheath is only a very thin ventral strip, and almost the whole of the perforated pharynx is presented to the cloacal cavity The surface layer of test is very thin but the basal layer is thicker, containing abdomina and some zooid-free test. The surface of the colony sometimes has a fluffy appearance but when spicules are more crowded it is hard and branchial apertures are depressed into the surface, dimpling it. Colonies are white in preservative with white to beige or yellow zooids. A bladder cell layer was not detected.

Spicules are spherical, and globular, generally to 0.04mm but occasionally to 0.06mm in diameter, with thin, crowded, radially arranged rod-like, flat- to round-tipped rays. The spicules are crowded in the test and are not interrupted around the stellate apertures.

ZOOIDS. Zooids are small, the thorax only 0.3mm long and the abdomen about the same size. Six distinct pointed lobes surround the branchial aperture. The atrial aperture is wide and most of the branchial wall is directly exposed to the cloacal cavity. A narrow atrial tongue, slightly bifid at the tip, projects from the upper rim of the aperture. A tapering retractor muscle is free from about halfway down the oesophagus. In the branchial sac 6 stigmata are in the anterior row, the next 2 rows have 5 each, and the last row has 4. The gut loop is relatively short, the ascending limb looping up over the gonads. The testis is hemispherical, its outer surface completely covered by the 6 coils of the vas deferens.

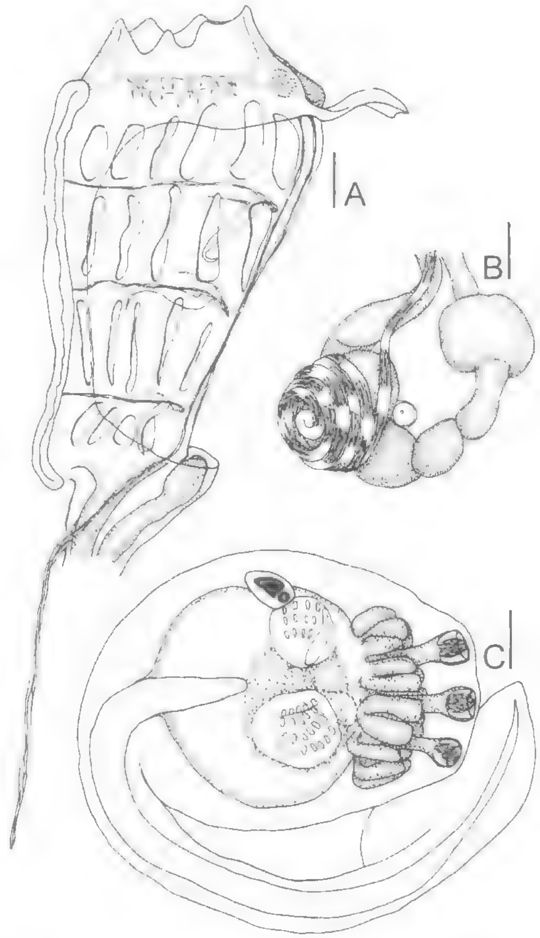


FIG. 109. *Didemnum precocinum* sp. nov. (QM 308026) – A, thorax; B, gut loop and gonads; C, larva. Scales: 0.1mm.

Larvae are present in specimens collected in March (QM G308026, G308028, G308156). The deep larval trunk is 0.7mm long with the tail curved a little more than halfway around it. Four or 5 lateral ampullae, along each side of the 3 antero-median adhesive organs, subdivide to 8 – 10 lateral ampullae per side in the fully developed larva. A large horizontal ampulla is on the left side of the trunk. A blastozooid is present in the

larval trunk. Some larvae are being released into the cloacal cavity (QM G308156).

REMARKS. The larva of the present species, with its numerous lateral ampullae and a blastozooid, is reminiscent of *Polysyncraton*. In *Didemnum* this type of larva is known for *D. arancium*, *D. chartaceum*, *D. jedanense*, and *D. levitas* from which the present species is readily distinguished by its spicules.

D. albopunctatum and *D. fragile* have similar (albeit smaller) globular spicules to those of present species, and their colonies show the same colour variation (white, grey, orange, vermilion). In *D. albopunctatum*, magenta is a fourth variant. Colour does not appear to constitute a species distinction. However, in addition to its different larva, *D. precocinum* has fewer vas deferens coils than either *D. albopunctatum* or *D. fragile*.

The pink shore specimens of *D. candidum*: Hastings, 1931 from Low Is (Thalamita Flat and R.C.: see Stephenson et al., 1931) possibly are specimens of the present species, having burr-like spicules crowded throughout. Other specimens Hastings (1931) assigned to *D. candidum*, viz. the white colonies with less crowded spicules (possibly *D. fragile*) and the dredged specimens with stellate spicules, are not conspecific with *D. precocinum*.

Didemnum psammatode (Sluiter, 1895)
(Figs 110, 168A; Pl. 14A-D)

Leptoclinum psamathodes Sluiter, 1895: 171: 1905b: 20.
Leptoclinum psammatodes: Sluiter, 1905a: 103.
Didemnum psammatodes: Sluiter, 1909: 46; 1913: 75. Michaelsen, 1919: 14 (part, vars *guinense*, *skeati*). 1920: 22 (part, vars *skeati*, *typicum*). Hastings, 1931: 95. Kott, 1962: 326 (part, var. *skeati*); 1981: 173; 1998: 83. Eldredge, 1967: 200.
Didemnum? psammatodes: Millar, 1956: 922.
Hypurgon skeati Sollas, 1903: 729. Herdman, 1906: 337.
Hypurgon fuscum Oka, 1931: 287.
Didemnum fuscum: Tokioka, 1953: 192.
Not *Didemnum fuscum* Sluiter, 1909: 52.
Didemnum dorotubu Tokioka, 1967: 74.

NEW RECORDS. South Australia (Yorke Peninsula, SAM E2611, QM G300972). Queensland (Capricorn Group, QM G308143, G308148, G308177, G308276, G308328; Swain Reefs, QM G305370, G305414, G305596, G305808; Whitsunday Is, QM G300943; Bowden Reef, QM GH5352; Lizard I., QM G308448). Northern Territory (off Cape Wilberforce, QM G302903).

PREVIOUSLY RECORDED. Victoria (Western Port, MV F68746, F68756 – Kott, 1962). Queensland (Moreton Bay, Sarina – Kott, 1962; Low Is – Hastings, 1931; Torres Strait – Kott, 1962). Indian Ocean (Red Sea – Sluiter, 1905, Michaelsen, 1920, Millar, 1956; Sri Lanka – Herdman, 1906). Western Pacific (Thursday I. – Sluiter, 1895; Indonesia – Sluiter, 1909 1913, Sollas, 1903; China, Philippines – Tokioka, 1967; Japan – Oka, 1931, Tokioka, 1953; Ifaluk Atoll – Eldredge, 1967; Fiji – Kott, 1981).

The species is a common component of the rubble fauna at most locations on the Great Barrier Reef and on many substrates at mainland locations. However, being relatively easy to identify in the field, it is seldom collected and, in this case, the small number of new records (referring only to specimens actually in collections) is not, an accurate reflection of its occurrence either in tropical or temperate regions.

COLONY. Colonies form thin encrusting sheets, although sometimes they are produced into fleshy lobes, or have irregular twig-like branches up to 8cm long and 1cm diameter (QM GH5352, G300972) and one colony (QM G300943) is a mass of cylindrical stalks that branch and coalesce forming a three-dimensional reticulum. All have characteristically restricted thoracic common cloacal cavities and the test, including the central test in the cylindrical stalks, has faecal pellets embedded throughout. Colour varies according to these crowded faecal pellets. In coral reef habitats colonies are opaque and cream coloured, in muddy habitats they are brown. Often, Chlorophyta are embedded in the surface, as well as in the basal test, amongst the faecal pellets. A conspicuous superficial layer of bladder cells is on the surface.

Spicules are never crowded, and are most numerous in the surface test around the branchial apertures. They are small, never exceeding 0.035mm in diameter, and diverse. Some have 11–13 relatively short, conical pointed rays, their bases separated from one another on the central spherical test mass; and others are burr-like with more numerous, much longer and cylindrical, or fusiform, or paddle-shaped rays and a ray/spicule diameter ratio about 0.4. Sometimes the long, pointed rays are different lengths. Cloacal canals are shallow and thoracic.

ZOOIDS. Zooids are minute, less than 1mm long. The atrial aperture is wide, exposing much of the branchial sac directly to the cloacal cavity. The branchial sac has 8 stigmata in the first row but numbers in other rows could not be counted accurately. The retractor muscle is free from halfway down the oesophagus. The gut loop is bent at right angles to the long axis of the thorax. The testis is a wide lens-shape, with the vas deferens wound around its outer surface 6 times.

The larva has been reported in specimens collected from Heron I. in September (QM G308276), the western Pacific in October (Eldredge, 1967), Mozambique (Millar, 1956). The larval trunk is about 0.4mm long, 4 lateral

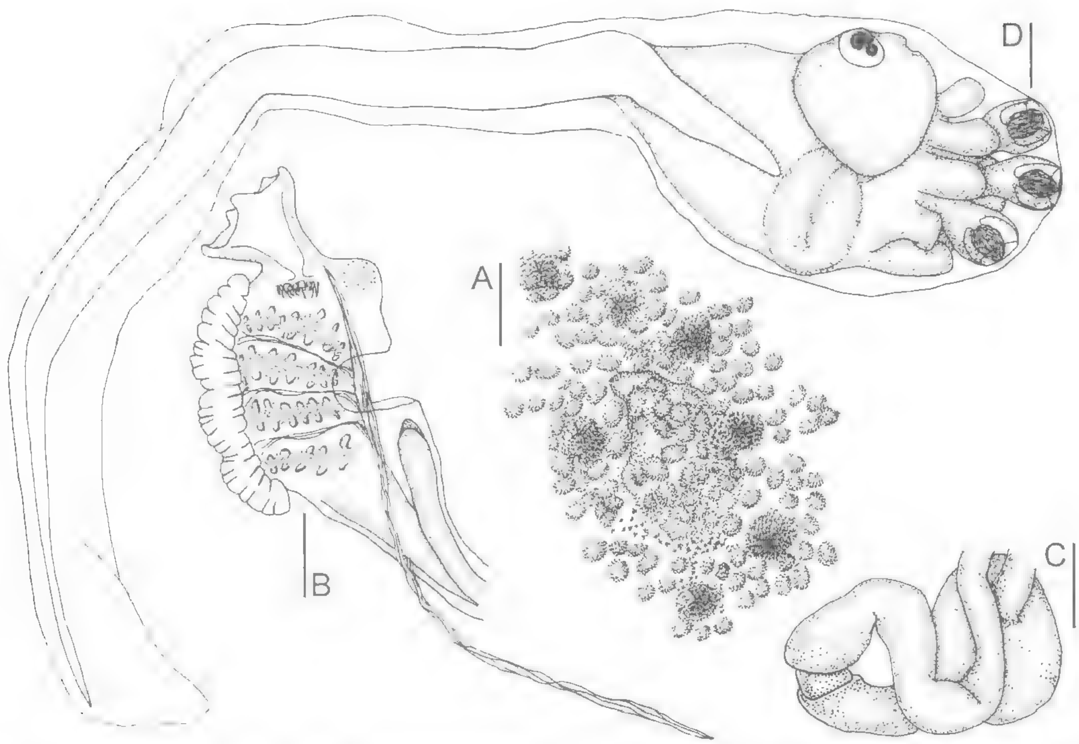


FIG. 110. *Didemnum psammatode* (A, QM G308177; B–D, QM G308276). A, surface showing small spicules scattered around branchial apertures in surface test and oval faecal pellets; B, thorax; C, gut loop; D, larva. Scales: A, 0.5mm; B–D, 0.1mm.

ampullae are on each side of the 3 antero-median adhesive organs, an otolith and an ocellus are present, and the tail is wound two-thirds to almost the whole way around the trunk.

REMARKS. Although Eldredge (1967) was of the opinion that the pellets embedded in the test are not faecal, they appear to be composed of the type of sediment that prevails in each respective habitat, which supports the view that they are.

The proposed synonymy (with the present species) of species without enclosed faecal pellets in the test (Michaelsen, 1920; Kott, 1962; Eldredge, 1967) is unjustified, as the small size and form of the spicules and their distribution in the surface test around the branchial apertures and the presence of faecal pellets are unique. How faecal pellets are incorporated into the test rather than being released into the common cloacal cavity is not known.

The spicules with long rays of slightly different length resemble those of *D. fucatum* but are smaller and the rays are more numerous. The spicules have more rays and are also smaller than those of *D. jedanense* and *D. theca* which they otherwise resemble. *D. stercoratum* Monniot & Monniot, 1996 has similar small zooids, larvae, spicules and faecal pellets in the basal test. However, in the present species faecal pellets always are crowded throughout and the species are not considered conspecific.

Sluiter (1909) drew attention to his initial mistake in the spelling of the species name.

Didemnum roberti Michaelsen, 1930
(Figs 111, 172B; Pl. 14E–H)

Didemnum roberti Michaelsen, 1930: 516. Kott, 1998: 83 (part, Shark Bay only).
Not *Didemnum roberti*: Kott, 1976: 68; 1998: 83 (part, Great Australian Bight and Bass Strait records <*D.ternerratum*).
Didemnum spongioides: Kott, 1962: 318; 1998: 83 (part, colonies from Rottnest I.).

NEW RECORDS. Western Australia (Monte Bello Is, QM G302937; Hut Point 13°55.7S 126°00.5E, QM G300924; Cape Lambert, WAM 526.92; Bonaparte Archipelago, QM G302932; NNE Dampier, WAM 524.92; NW Enderby I., WAM 954.88). Queensland (Cockburn Reef, QM G302851). Northern Territory (Gulf of Carpentaria, QM G300827; Groot Eylandt, QM G313569; Parry Shoals, Bathurst I., QM GH5359, G302907).

PREVIOUSLY RECORDED. Western Australia (Shark Bay – Michaelsen, 1930; Rottnest I. – Kott, 1962).

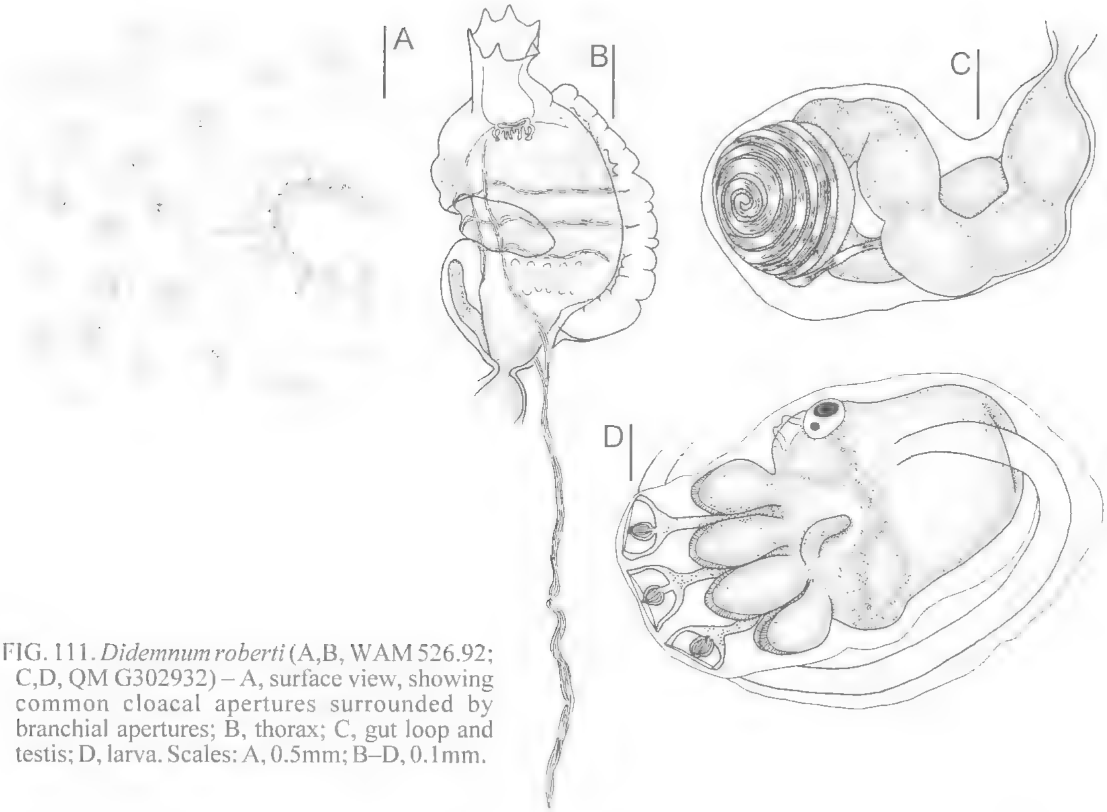


FIG. 111. *Didemnum roberti* (A,B, WAM 526.92; C,D, QM G302932) – A, surface view, showing common cloacal apertures surrounded by branchial apertures; B, thorax; C, gut loop and testis; D, larva. Scales: A, 0.5mm; B–D, 0.1mm.

COLONY. Colonies are encrusting sheets, or thick slabs or various large sponge-like masses of fan- or dome-shaped to branching and anastomosing vertical lobes. The lobes are generally oval in section, to 30mm long, and up to 2cm diameter, or fleshy digitiform lobes and lamellae that project into domes or ridges with terminal common cloacal apertures on the upper surface.

The outer surface is smooth and even. The test is firm, but gelatinous and translucent. Spicules are crowded in a layer at the surface, making it raspy to the touch and opaque. The surface layer of spicules is interrupted by the branchial apertures. Although a small clump of spicules is in each siphon, spicules do not outline the apertures, which are not conspicuously stellate. Beneath the crowded surface layer, spicules are less crowded and sometimes even sparse although there usually is a thin but patchy layer around the common cloacal canals. Spicules are stellate with 7–9 and occasionally only 5 long, attenuated, sharply pointed, spiky rays in optical transverse section, generally to 0.05mm but occasionally up to 0.09mm in diameter. There are occasional spicules with truncated rays. The ray length/spicule diameter ratio is up to about 0.375.

The common cloacal cavity is a labyrinth of relatively shallow posterior abdominal canals separating the zooid-bearing layer from the basal test or a central test core. Zooids, in clumps at the surface, are crowded and parallel to one another. The common cloacal cavity continues up around each clump of zooids and penetrates it at thorax level. Clumps of zooids are not obvious from the surface of the colony, possibly because the whole colony and the cloacal canals are held open by the firm and rigid test.

In preservative, the holotype is opaque and yellowish grey (Michaelsen 1930). Newly recorded specimens from the Bonaparte Archipelago, Parry Shoals and Cockburn Reef are grey, becoming more intense and almost black on the top of each lobe. Black pigment, is in quite large opaque, oval granular cells in the test at abdominal level, underneath the translucent whitish test around the thoraces. It forms a black-grey middle layer through the colony in several of the preserved specimens. The specimen from Hut Point (QM G300924) is

reported as white, although the in situ photograph has orange flecks. The robust, lobed specimen from Groot Eylandt (QM G313569), in preservative, has spots and irregular patches of black pigment more crowded toward the top of the lobes, but was black and yellow in life.

ZOOIDS. All newly recorded specimens except QM G300827 (which appears to have been frozen) have well preserved zooids. They are about 1.5mm long, of which the thorax is about 0.8mm. The branchial siphon is long and cylindrical, reaching through the crowed surface layer of spicules. The atrial opening with a narrow bifid anterior lip is large, exposing most of the branchial sac to the cloacal cavity. The thorax is small and narrow. According to Michaelsen (1930), 7–10 stigmata are in each row. Nine were accurately counted in the anterior row of newly recorded specimens (QM G302937). A long, often ribbon-like retractor muscle projects from the top of the oesophagus. The gut is bent at right angles to the longitudinal axis of the thorax. The testis is large, undivided and lens-shaped to spherical, with 8 coils of the vas deferens around it.

Tailed larvae were found in the central or basal test of specimens (QM G313569, G300827) collected from the Gulf of Carpentaria in October and November respectively. They are most numerous in the former. The larval trunk is spherical, about 0.45mm in diameter. The anterior half is occupied by 4 pairs of lateral ampullae on each side of the usual 3 antero-median adhesive organs and the posterior half contain a deep vertical oozooid. The tail is wound about two-thirds of the way around the trunk.

REMARKS. Most newly recorded colonies are identical with the holotype (Michaelsen, 1930: 517, fig. 5). Despite Michaelsen's (1930) report of spicules with 12–15 rays in optical transverse section, he described spicules of similar form to those newly recorded with the diameter of the largest spicules about 0.04mm and with the same distribution. Possibly he overestimated the number of spicule rays.

Michaelsen (1930) drew attention to the resemblance of the present species to *D. spongioide* Sluiter, 1909, which, however, has zooid-free ridges on the surface, and bladder cells in the test. Probably the most significant distinctions are differences in surface morphology, distribution of spicules (present throughout the colony in *D. spongioide*, but largely confined to a crowded layer beneath the surface and sometimes a less crowded layer around the common cloacal cavity in the present species), and form of the spicules (with spiky attenuated rays in *D. roberti*, and blunt to almost rod-like rays in *D. spongioide)*. In *D. roberti* the central test mass may be an important structural element in the colony, in the absence of the surface ridges of *D. spongioide*. *D. caesium* has spicules similar in size, form and distribution to the present species, but has no posterior abdominal system of canals.

South Australian *D. fragum* has colonies, cloacal systems, larvae and zooids that are very similar to the present species but it has more and blunter spicule rays.

The zooids with a long branchial siphon resemble those of *D. elongatum*. However, the latter species has larger spicules, a longer branchial siphon, and an encrusting sheet-like colony. *D. spongioides*: Millar, 1975 (<D. ossium) has a similar colony and long branchial siphons but smaller spicules and a larva with numerous ectodermal ampullae.

The cloacal systems of both *D. roberti* and *D. spongioide* are similar to those in *Trididemnum sibogae* and *T. crystallinum*, both recorded from the Gulf of Carpentaria. However, in addition to their generic differences, both species of *Trididemnum* are distinguished from the present species by their spicules and folded, coalescing colonies.

D. roberti: Kott, 1976 from Western Port has encrusting colonies, 3-dimensional cloacal cavities, zooids with 8 coils of the vas deferens, and almost globular spicules to 0.04mm diameter with short rounded rays. As Kott (1976) suggested, the specimens are conspecific with *D. ternatanum*: Kott, 1972b (<*D. ternerratum*) from South Australia. *D. sucosum* from Western Port, has a similar colony but larger spicules without the spiky rays of the present species. *D. spongioides*: Kott, 1962 from Rottnest I. has a moderately slab-like colony, but otherwise all the features of the present species, including the posterior abdominal common cloacal cavity and pointed spicule rays.

Didemnum scopi sp. nov.
(Figs 112, 173B; Pl. 15A)

TYPE LOCALITY. Queensland (Capricorn Group, Heron I. north reef Gorgonia Pools, coll. P. Kott et al., 6.9.94, syntypes QM G308216, G308221, G308478).

FURTHER RECORDS. Queensland (Caloundra, QM G308463; Hervey Bay, QM G308473; Capricorn Group, QM G302304, G302332, G308023, G308109-10, G308114, G308116, G308126, G308140, G308147,

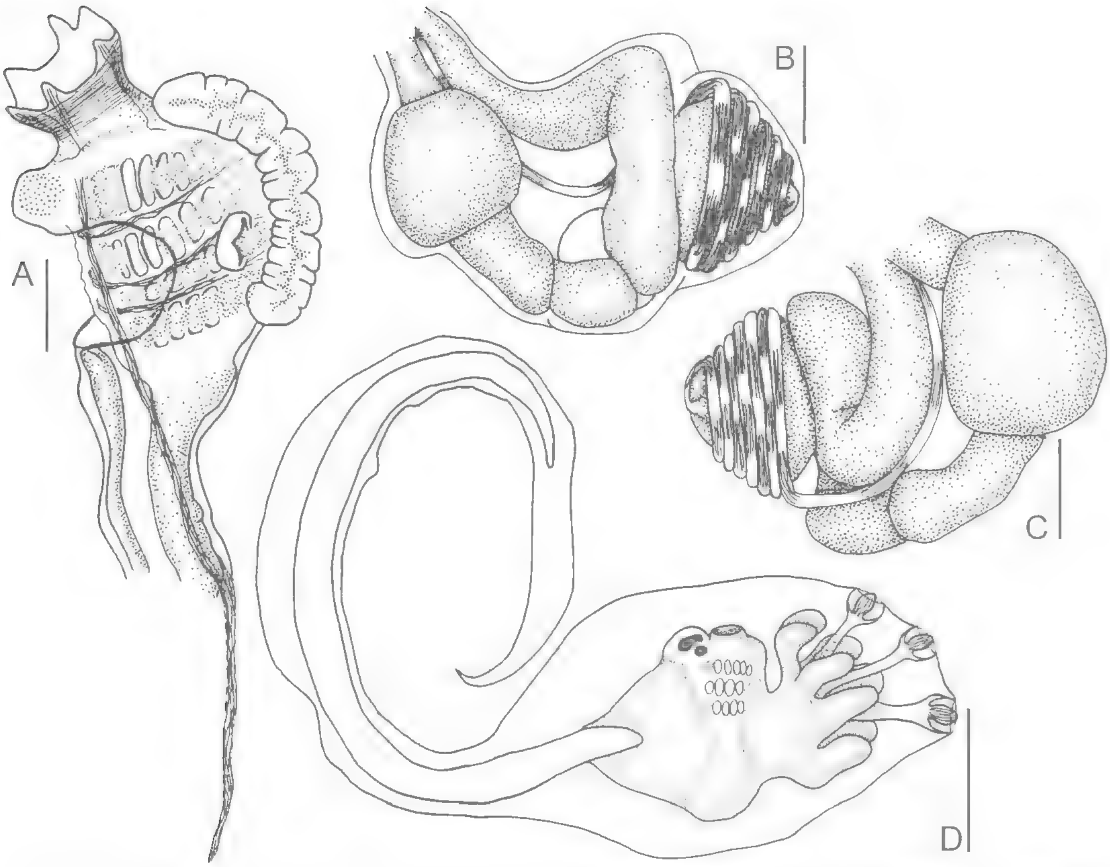


FIG. 112. *Didemnum scopi* sp. nov. (A,B, QM G308110; C, QM G308219; D, QM G308221) – A, thorax; B, ventral view of abdomen; C, dorsal view of abdomen; D, larva. Scales: 0.1mm.

G308158, G308168, G308173, G308180, G308184, G308209, G308213, ? G308219; Swain Reefs, QM G308377, G308396; Barron Point, QM G302269).

COLONY. Colonies are hard, encrusting sheets to slabs and occasionally small cushions with rounded margins (QM G308126). Sometimes large common cloacal apertures are on elevated ridges (QM G308116) or rounded swellings on the upper surface (QM G308168). Small spicule-filled papillae are on parts of the upper surface of some specimens (QM G308110, G308213) and others (QM G308140, G308209) have a hollow pointed papilla from the ventral side of each branchial aperture, which tends to cover the aperture when the zooid is contracted. A thin superficial bladder cell layer is conspicuous only around the margin of the colony. The cloacal cavity is thoracic, usually shallow, but occasionally deeper around a clump of zooids leaving the embedded abdomina projecting up into the common cloacal cavity (QM G308116). Branchial apertures may be conspicuously stellate with a margin of spicules or the spicules may be crowded around the openings and obscure them. The spicules usually are crowded throughout the colony, but occasionally are mixed with bladder cells creating a frothy appearance in the surface test. Sometimes they are present sparsely in the bladder cell layer and often they become sparse toward the base of the colony where they are mixed with bladder cells. Spicules are small, the largest being 0.05mm diameter, and relatively uniform, varying only in the number of long almost cylindrical or rod-like rays, 9–11 in optical transverse section. The rays have blunt pointed to rounded tips. Occasionally spicules have shorter, more conical rays separated from one another on the central mass.

Although one specimen (QM G308173) is magenta, most living colonies are some shade of red (geranium red[R], scarlet vermilion[R],

vermilion[R], or dragons blood red[R]) or orange (orange vermilion[R], orpiment orange[R], saturn red[R], ferruginous[R]). Colonies appear spotted in life because the zooids are brighter than the overall colour of the colony, the pigment in the superficial layer of test being diluted by the white spicules that underlie it. Zooids are orange (saturn red[R]), burnt carmine[R], red, apricot, or crimson, becoming orange and translucent in preservative. Common cloacal apertures have white rims where the red pigment is absent and white spicules are seen through the test.

ZOOIDS. Zooids are small (about 0.6mm) long. A short branchial siphon has 6 points around its rim. The atrial aperture is a wide, sessile opening without an anterior lip, and a retractor muscle projects from about halfway down a long oesophageal neck. Nine stigmata are in the first 2 rows, 8 in the third row and 7 are in the last row, although these usually are obsured by contraction. The post-pyloric part of the gut loop is bent ventrally creating a tight double loop, and the gut has the usual divisions of stomach, duodenum, posterior stomach and rectum.

Gonads are present in a number of specimens (QM G302304, G308109-10, G308168, G308173, G308219, G308221). The vas deferens coils 7 times around the small testis. Larvae, present in March (QM G308110) and September (QM G302269, G308219, G308221) are relatively small (trunk length 0.55mm) with 4 pairs of ampullae and the tail wound halfway around the trunk.

REMARKS. The species resembles other encrusting red or orange species with brightly pigmented zooids seen through the branchial apertures. It can be distinguished by its particularly small zooids with a long oesophageal neck, a double gut loop, and its unique spicules. Spicules are smaller than those of *D. moseleyi* (which also has a variety of spicules), but it lacks the globular spicules and sharply pointed rays of the latter species, and has more with long rays. *D. perplexum* can be distinguished by its larva and its spicules with fewer and more conspicuously conical rays. *D. clavum*, *D. cuculliferum*, *D. membranaceum* and *D. stragulum*, which, like several specimens of the present species often have a pointed papilla ventral to each branchial aperture, have different spicules and larger zooids. *D. candidum* has larger zooids and distinctive spicules with fewer rays. Spicules from one specimen (QM G308219) are up to 0.03mm diameter with 11–13 rays in optical transverse section and resemble those of *D. jedanense*, which differs in its cloacal systems and larvae (with numerous epidermal ampullae and a blastozooid).

Didemnum sordidum sp. nov.
(Figs 113, 173A; Pl. 15B,C)

Didemnum membranaceum: Kott, 1962: 323; 1998: 82. Kott & Goodbody, 1982: 518. Kott et al., 1984: 310. Monniot & Monniot, 1987: 36.

TYPE LOCALITY. Queensland (Noosa Heads, 1m, coll. P. Kott 02.05.61, holotype QM G4970; Heron I. north reef, coll. P. Kott 05.09.94, paratype QM G308304).

FURTHER RECORDS. Western Australia (Lord Mayor Shoal, QM G300942; Pilbara, QM G300932). Queensland (Point Lookout, QM G301525; Moreton Bay, QM G308451; Caloundra, QM G308453, G308464; Bargara, Noosa, Currumbin – Kott, 1962; Heron I., QM GH899, GH1336, GH1836, G308016, G308095, G308303-4, G308318; Swain Reefs, QM G305372; Lizard I., AM Z5117). Hong Kong (QM GH163 Kott & Goodbody, 1982). Philippines (QM GH481). French Polynesia (Monniot & Monniot, 1987). Indian Ocean (Christmas I., WAM 120.93).

COLONY. Most known colonies form thin, encrusting sheets. However, 2 large ones about 7cm diameter (QM G300932, G300942) consist of an erect thicket of narrow (to 5mm diameter) branches, that originate from a narrow base . The spicules are particularly crowded in the central rod of test in the branches of these colonies making a firm axis for the erect colony. Spicules are also present in the remainder of the colony, including the very thin, pigmented superficial layer of test. Round, sessile common cloacal apertures are scattered about 5mm apart over the surface and on the terminal free tips of the branched stalks. Abdomina are embedded around the periphery of the central core which is homologous with the basal test of an encrusting colony. Colonies are very hard, and the surface flat and smooth although some white streaks and low ridges occur where especially crowded spicules exclude the pigment. Some large vesicles in the surface also exclude the pigment. The test is soft and readily breaks up. Superficially a very thin coat of bladder cells and pigment is present in some parts, but pigment often is absent and white spicules are exposed. Living colonies have orange-chrome[R] to brownish-orange pigment in patches and long streaks alternating with streaks of white to grey which occur especially around the common cloacal apertures where pigment is absent and spicules are exposed. Zooids are vermilion[R]. *Prochloron* often is on the surface. The cloacal

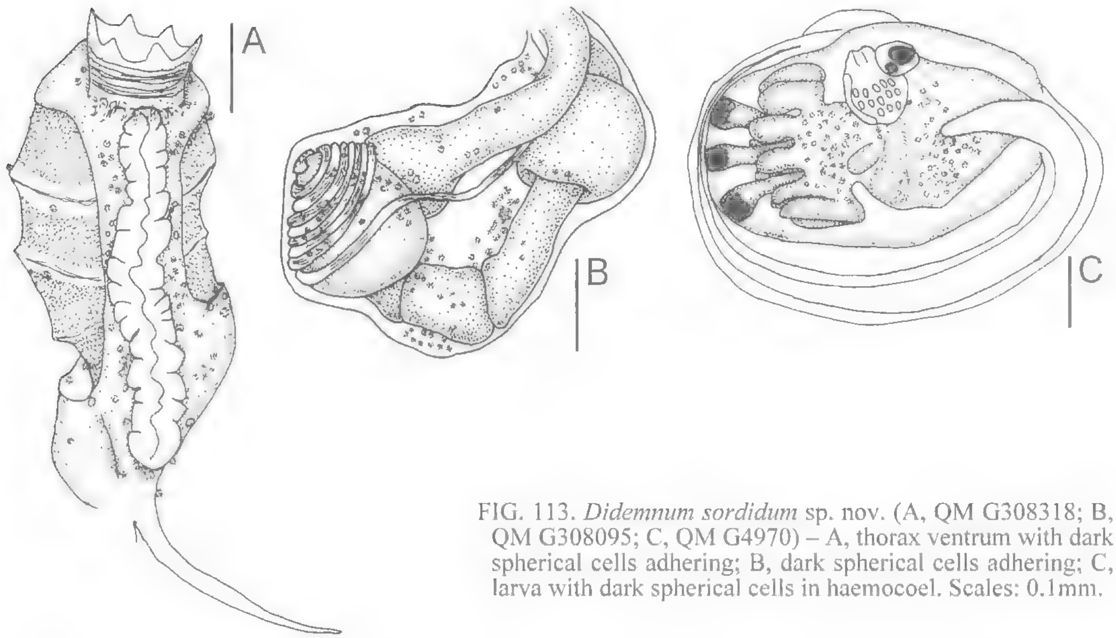


FIG. 113. *Didemnum sordidum* sp. nov. (A, QM G308318; B, QM G308095; C, QM G4970) – A, thorax ventrum with dark spherical cells adhering; B, dark spherical cells adhering; C, larva with dark spherical cells in haemocoel. Scales: 0.1mm.

cavity is thoracic and relatively shallow. Spicules are crowded throughout the test and in the linings of the branchial siphons, forming a white spot in the centre of a relatively spicule-free area around each branchial aperture. In preservative, large (up to about 0.015mm diameter) brown cells with granular contents lie in the colony, around the zooids, in the common cloacal cavity and in the test. Internally they confer a dark colour on the preserved colony.

Spicules are relatively large, to 0.065mm in diameter, with conical rays, 9–11 in optical transverse section. Mostly the rays have pointed tips but others are slightly rounded. Occasional spicules have fewer rays (as few as 7) with each one seated in a distinctive pentagonal base.

ZOOIDS. Zooids are small, about 0.6mm when contracted. The branchial siphon is relatively long and cylindrical with 6 small points around it. The atrial aperture exposes most of the branchial sac directly to the cloacal cavity. The thorax is narrow with only about 6 stigmata in the middle rows of the branchial sac. A retractor muscle extends from a short distance down the oesophagus. The gut loop has the usual long duodenum, oval posterior stomach and a rectum that is wide at its proximal end. The distal end of the gut loop is flexed ventrally. The testis is against the posterior surface of the flexed gut loop. It is sometimes lens-shaped, but occasionally pointed where it joins the vas deferens, which coils 8 times around the outer half of the testis.

Larvae are in the test of specimens collected in May from Noosa (Kott, 1962). They are small, the trunk being 0.35–0.45mm long. Five lateral ampullae are along each side of the 3 median adhesive organs. The large granular brown cells are in the larval haemocoel.

REMARKS. Generally the characteristics of this species that help to distinguish it are the orange colour of the living colonies streaked with white and grey, the dark brown colour of the internal part of the preserved colony, the small zooids and larvae and the large number of vas deferens coils. The 2 large colonies of narrow stalk-like branches are conspicuously different from encrusting sheets. Nevertheless the colony form is the only difference detected and specimens of both forms are here treated as conspecific. The upright branches may be a growth form that occurs in more advanced colonies in response to some environmental factor such as the less restricted habitats available in deeper waters.

D. fuscum has a similar larva with brown cells in the haemocoel and 5 pairs of lateral ampullae, and a similar number (9) of vas deferens coils. The present species is distinguished from it by the characteristic orange and grey colour pattern of living specimens, and the smaller spicules, with relatively numerous but shorter, broader and more distinctly conical rays sometimes set in

pentagonal bases. The loose brown cells, numerous vas deferens coils and conical spicule rays occur in temperate *D. spadix* which is distinguished mainly by the vesicles surrounding each branchial aperture rather than being scattered in the surface. Similar brown cells also occur in other species (see Glossary, **haemocoel**).

Some spicules resemble *D. digestum*, having conical tips set in a pentagonal base, but in *D. digestum* the rays are larger and fewer.

Didemnum spadix sp. nov.
(Figs 114A,B, 169E; Pl. 15D)

Didemnum candidum: Kott, 1972b: 179; 1975: 9.

TYPE LOCALITY. South Australia (Elliston Bay 6m, roof of caves, strong surge, coll. S. Shepherd 13.5.71, holotype SAM E2841; northern Great Australian Bight 32°24'S 133°30'E, 49m, coll. Prawn Expedition 23.8.73, paratype SAM E2694).

FURTHER RECORDS. Western Australia (Busselton Jetty 6-8m, SAM E2686). South Australia (Elliston Bay – SAM E2700 Kott, 1972b); ? New South Wales (Illawarra, QM G308094).

COLONY. Colonies form rather irregular fragile, thin sheets with spicules crowded throughout excluded only by the circles of about 10 large spherical vesicles that surround each conspicuously stellate branchial aperture. The crowded spicules continue down into the siphon linings without interruption. Spherical brown pigment cells (about 0.008mm diameter) are mixed with the spicules in the test and especially are present adhering to the body wall around each zooid. In preservative the colonies are slightly brownish-yellow on the upper surface owing to patches of these brown cells that probably have escaped from the internal test. Otherwise the test is white with crowded spicules and the brown-coloured zooids show through breaks in the surface and through the branchial apertures. The preservative is stained brown, and this persists over nearly 30 years.

The cloacal cavity is horizontal and thoracic, each thorax crossing it with a ventral sheath of test. The surface layer of test is thin, but the basal layer (in which abdomina are embedded) is thicker. Spicules are stellate, rarely to 0.45mm in diameter but usually less, and with 7–9 and occasionally 11 conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.35. The conical tips of the rays are set in a thick basal shaft, or in the central mass.

ZOOIDS. Zooids are small, less than 1.0mm long (about 0.7mm). The branchial siphon is well developed with 6 pointed lobes around the rim of the opening. The atrial aperture is wide and exposes the branchial sac directly to the common cloacal cavity. An atrial tongue is not present. A long, finely tapering retractor muscle projects from the upper part of the oesophageal neck. In those zooids in which the stigmata could be counted (SAM E2686), there are not more than 6 per row. The gut loop is of the usual form, the post-pyloric part bent ventrally, and the large, undivided testis, with 8 coils of the vas deferens around it, lies against the dorsal side of the ventrally flexed part of the loop. Larvae are not known.

REMARKS. Although Kott (1972b) referred to dark brown zooids with blackish-brown pigment cells in the Elliston Bay specimen she had mistakenly assigned to *D. candidum*, this pigment is not in the re-examined specimen, and probably is lost in preservative. She recorded 8 coils of the vas deferens around an undivided testis, although these also were not detected upon re-examination. The circles of vesicles she recorded remain intact.

The large vesicular cells regularly arranged around each branchial aperture resemble those of *Polysyncraton orbiculum* and *P. circulum*. The species is a *Didemnum*, however. It resembles tropical *D. fuscum* and *D. sordidum* in most characters including the small zooids with relatively few stigmata, relatively numerous coils of the vas deferens and the dark spherical cells that lie free in the space between the test and the zooids and cling closely to the body wall (see Glossary, **haemocoel**). Spicules of the present species have about the same number of rays as *D. fuscum*, but are shorter and more conical (like the rays of *D. sordidum*). The spicule rays of *D. sordidum* are more numerous, and its spicules are larger (up to 0.065mm diameter). Also, *D. sordidum* and *D. fuscum* lack the large vesicular cells in the surface.

A thin, flat colony with spreading margins from New South Wales (QM G308094) lacks the vesicular cells in the surface test, and the spherical brown cells in the test. Nevertheless its zooids are brownish, it has diffuse brown pigment in the surface test, and its spicules are identical with those of the present species, to which it has been questionably assigned.

Didemnum spongioide Sluiter, 1909
(Figs 114C–E, 171E; Pl. 15E)

Didemnum spongioides Sluiter, 1909: 67; Monniot, 1995: 326.

Not *Didemnum spongioides*: Kott, 1962: 318; 1998: 83 (part, from Rottnest I., <*Didemnum roberti*; part, from Tasmania <*Didemnum sucosum*). Eldredge, 1967: 193. Millar, 1975: 231 (< *D. ossium*).

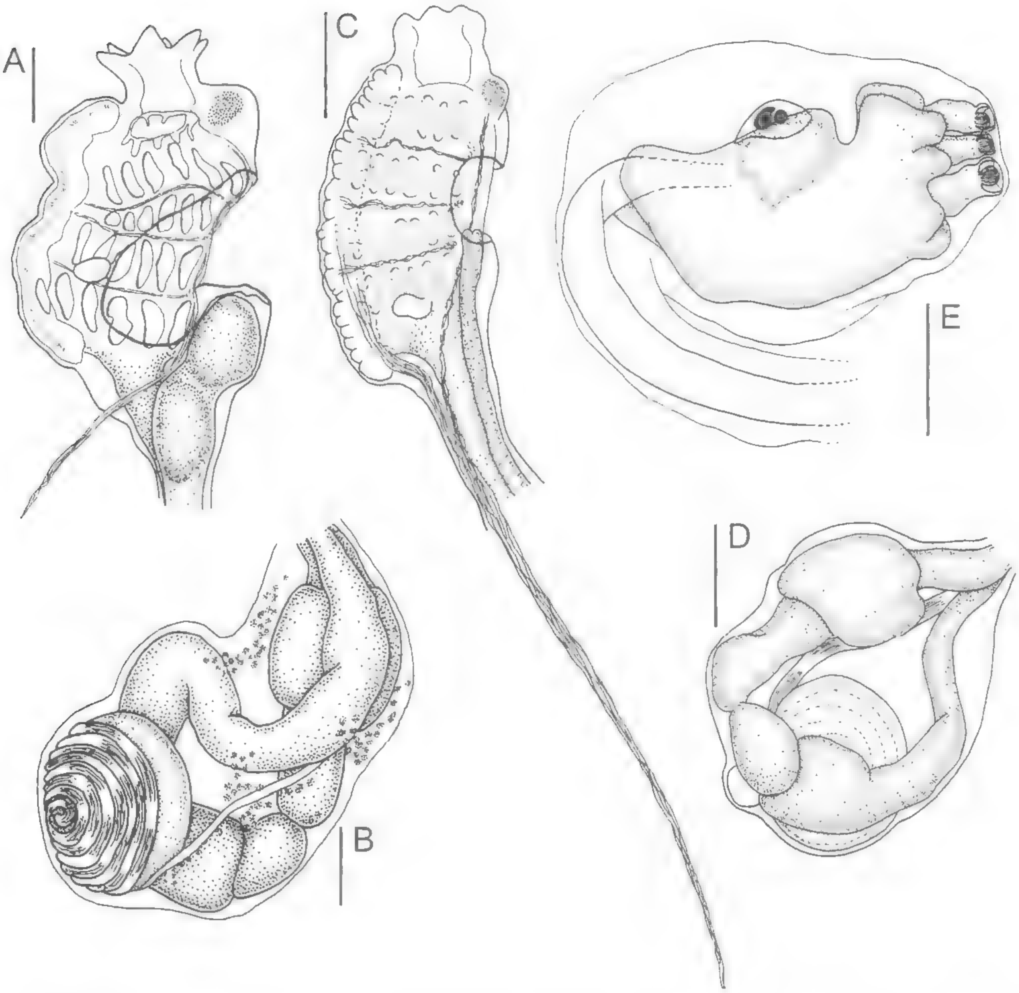


FIG. 114. A, B, *Didemnum spadix* sp. nov. (A, SAM E2686; B, SAM E2841) – A, thorax; B, abdomen showing dark spherical cells around the outside. C–E, *Didemnum spongioide* (QM GH5343)–C, thorax; D, gut and gonads ventral view; E, larva. Scales: 0.1mm.

NEW RECORDS. Queensland (Torres Strait, QM GH5343). Northern Territory (Grose Is, 2 n.miles W of Bass Reef, QM G303536, G303559, G303574, G303631-2, G303635, G303638, G303640, G303679).

PREVIOUSLY RECORDED. Indonesia (Aru Is – Sluiter, 1909). New Caledonia (Monniot, 1995).

COLONY. The largest colonies are to 20cm high, composed of long, vertical, parallel, but very irregular lamellae and cylinders with sharp vertical ridges and points along their outer surface. The branchial apertures open to the surface between the surface ridges. The colony lobes anastomose with one another here and there along their length. The whole colony is sponge-like, and the terminal common cloacal aperture at the top of each lobe contributes to its sponge-like appearance. The surface layer of test forms a very thin cover over the common cloacal cavities, which are part of a particularly extensive labyrinth of spaces of thoracic and posterior abdominal spaces that perforate the internal test. The colony is sponge-like in consistency and appearance.

Spicules occur throughout, but are not crowded and the test is translucent. They are stellate, to 0.078mm diameter, with 7–9 long only slightly tapering, rather blunt-tipped rays in optical transverse section. The ray-length/spicule diameter ratio is about 0.38.

ZOOIDS. Zooids are robust, their length, even with thorax contracted, is more than 1.0mm. At least one-third of the body length is a long

oesophageal neck. The branchial aperture has 6 rounded lobes and is on a short siphon. The atrial opening is wide and sessile, without a tongue. Strong muscles are in the body wall, and zooids of the known specimens are strongly contracted. A thick, straight retractor muscle projects from about halfway down the oesophageal neck. The branchial sac has 4 rows of stigmata but the number in a row was not determined. The posterior pyloric part of the gut loop is relatively short and rounded, with a short duodenum, posterior stomach and a much enlarged proximal part of the rectum. The undivided testis is surrounded by 7 coils of the vas deferens.

Larvae are small with a trunk 0.3–0.375mm long, and 4 pairs of lateral ampullae each side of the 3 antero-median adhesive organs. The tail is wound about three quarters of the way around the trunk in larvae from New Caledonian (Monniot, 1995), although the newly recorded specimen from Queensland (QM GH5343), collected in May, has the tail wound about one and a quarter times around the trunk.

REMARKS. The newly recorded colonies have sharp, toothed, ridges extending along the length of the lobes and look exactly like the New Caledonian colonies (Monniot, 1995) and the one photographed by Sluiter (1909: 68).

The assignation of colonies to this species by Kott (1962) and Eldredge (1967) was based on a posterior abdominal cavity, which was (wrongly) thought to be unique in *Didemnum*. The colony lobes of *D. spongioides*: Kott, 1962 from Rottnest I. and Tasmania have posterior abdominal cloacal cavities, spicules crowded in a thin surface layer of the colony but less crowded in the remainder of the test and smooth colony surfaces without the sharp, toothed, ridges of the present species. The colonies from Rottnest I. are *D. roberti* and the Tasmanian material is a previously undescribed species, *D. sucosum*. *D. spongioides*: Eldredge, 1967 has flat colonies with spicules crowded throughout, and only narrow posterior abdominal cavities and its affinities are not known.

Sluiter (1909) discussed the relationship of the present species to *D. ceylonicum* (Herdman, 1906), which has branches of the same sponge-like nature. However the colonies from Sri Lanka are encrusting, the irregularities resulting from growth over rubble, which becomes incorporated in the test.

D. spongioides: Millar, 1975 and the apparently conspecific *D. misakiense*: Tokioka, 1967, both from the Philippines, have massive lobed colonies resembling the present species. They are distinguished by their smooth surface, central test core, thicker surface test with longer branchial siphons, less complex colonies in which the branches and lobes do not coalesce and smaller spicules (up to 0.04mm in diameter) with more numerous conical pointed rays in optical transverse section. Millar (1975) reported large larvae with a blastozooid and about 17 pairs of lateral ampullae per side. These colonies are *D. ossium* (see also *D. roberti*, Remarks).

Didemnum stragulum sp. nov.
(Figs 115A–C, 171G)

Didemnum makropnous Sluiter, 1909: 56 (part, Station 313).
Didemnum cuculliferum: Monniot, 1995: 305.

TYPE LOCALITY. Eastern Indian Ocean (SW side of West I. off S end airstrip Cocos (Keeling) Is, intertidal coll. L. Marsh 20.2.89, holotype WAM 610.89).

FURTHER RECORDS. Queensland (Heron I., QM G302096 G308009). Indonesia (Bali Sea – ZMA TU461.6 Sluiter, 1909). West Pacific (New Caledonia – Monniot, 1995).

COLONY. The colony is a tough, leathery sheet with the surface depressed over common cloacal canals that surround elevated, usually zooid-free circular, elongate or irregular stands of test. Zooids are along each side of the common cloacal canals, their ventral surface embedded in the solid test. The common cloacal canals are deep, extending the full length of the zooids. Except in one specimen from Heron I. (QM G308009) in which the zooids are regressed, the surface test is raised into a spicule-filled pointed papilla on the ventral side of each stellate branchial aperture, and these emphasise the double rows of zooids surrounding each elevation of the colony surface. Spicules are crowded throughout the colony although they are absent from the base. Brown pigment particles are in ribbon-like groups in the surface test amongst the spicules. A Heron I. specimen (QM G302096) was heliotrope purple[R] in life with deeper colour in the depressions between the elevated areas of test.

Spicules are large (to 0.12mm diameter) and cause the surface of the colony to feel raspy. They have 7–9 and occasionally 11 pointed conical rays in optical transverse section. The ray length/spicule diameter ratio is about 0.27.

ZOOIDS. The branchial aperture is short and wide and the thorax is robust with about 9 stigmata per row. A long tapering retractor muscle projects from about halfway down the oesophageal neck. An atrial tongue is not present. The gut loop has

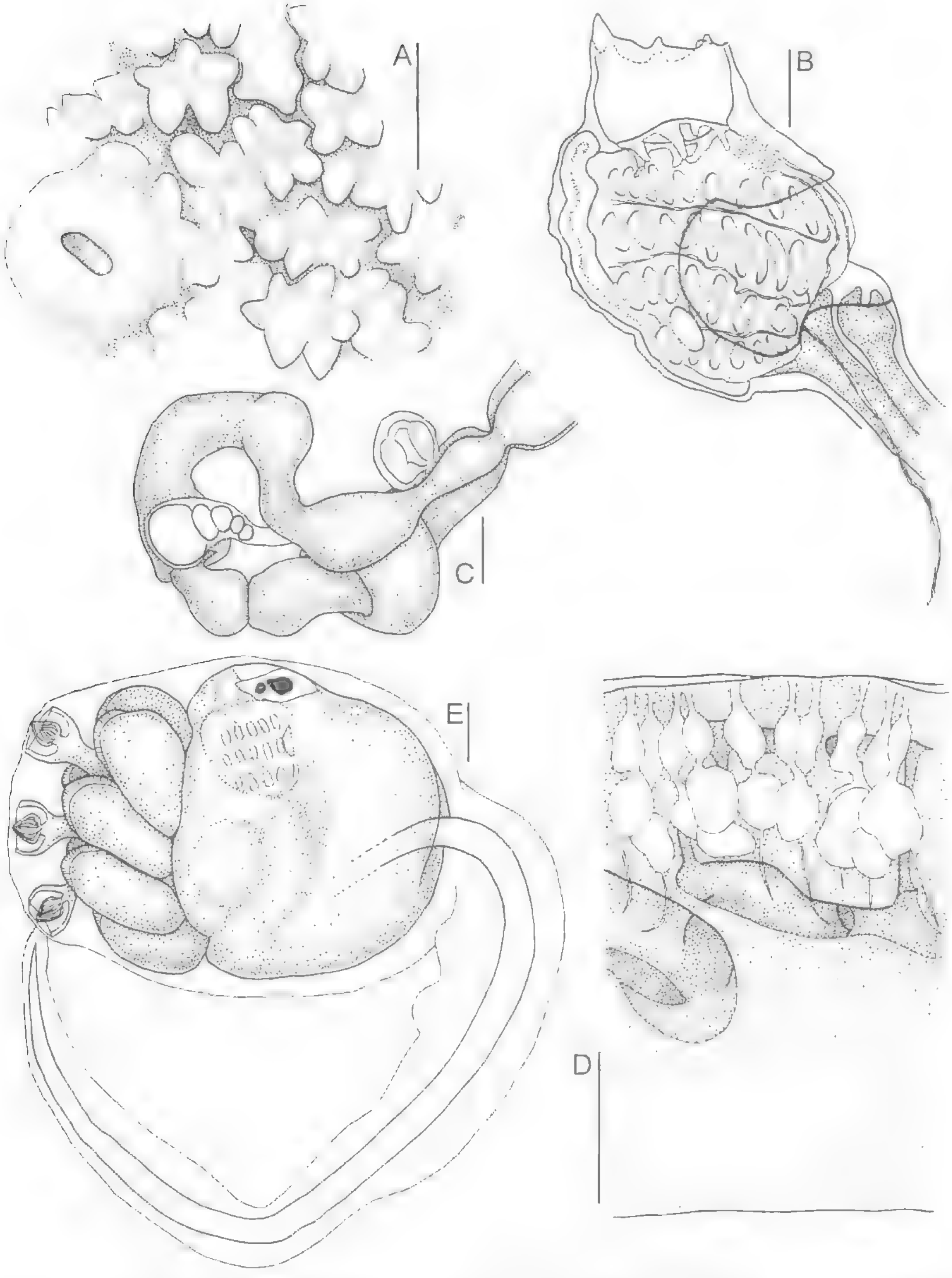


FIG. 115. A–C, *Didemnum stragulum* sp. nov. (A,C, WAM 610.89; B, QM G302096) – A, part of surface showing papillae associated with each branchial aperture and a common cloacal opening; B, thorax; C, dorsal view of abdomen with gut loop, ovary and an oesophageal bud. D, E, *Didemnum sucosum* sp. nov. (D, QM G300980; E, AM U182) – D, semidiagrammatic vertical section; E, larva. Scales: A, 2.0mm; B,C,E, 0.1mm; D, 0.5mm.

the form usual in this genus. Zooids in the holotype are all in active replicating mode and gonads were not detected. Mature testes, present in one specimen (QM G302096), have 6 coils of the vas deferens (Monniot, 1995 reported 5 to 9). Larvae from New Caledonia have 4 pairs of epidermal ampullae in a trunk of variable length.

REMARKS. The large spicules distinguish it from *D. cuculliferum* and others with similar pointed papillae that close down over the branchial apertures. *D. cygnuus*, *D. macrosiphonium*, *D. patulum* and *D. tonga* have similar colonies (with zooids lining the common cloacal canals that surround often protuberant zooid-free test areas) but they have smaller and different spicules. The temperate *D. microthoracium* has much in common with the present species, although its spicules are smaller, its circular cloacal canals more regular and restricted and the surface elevations of the zooid-free areas not so conspicuous. *D. grande* has a similar cloacal system and similar spicules, although the latter are not quite so large, only occasionally reaching 0.1mm in diameter. *D. caesium* has black pigment in the colony, spicules missing from the middle layers of the colony, an atrial lip and a different cloacal system. Of the species with large stellate spicules, *D. stragulum* is the only one with a pointed papilla associated with the ventral lobe of each branchial aperture. The heliotrope[R] colour of this species is most like *D. viride*.

One of the syntypes of *D. makropnous* Sluiter, 1909 (ZMA TU461.6), has all the characters of the present species including the surface pointed papillae, spicules to 0.110mm diameter, zooids along each side of circular common cloacal canals and large thoraces. Its location, just north of Sumbawa is not so far distant from the type location of the present species.

D. cuculliferum: Monniot, 1995 has large stellate spicules that are not found in *D. cuculliferum* but are similar to the present species which has similar surface papillae. The large larvae (the trunk 0.7mm long) with 4 pairs of ectodermal ampullae are also alike and the material from New Caledonia cannot be distinguished from the present species.

Didemnum sucosum sp. nov.
(Figs 115D,E, 170B; Pl. 15F)

Didemnum spongioides: Kott, 1962: 318; 1998: 83 (part, specimens from Tasmania).

TYPE LOCALITY. Victoria (Western Port, 38°24.6S 145°25.5E Corinella Jetty piles, wood/mud substrate, coll. AIMS Bioactivity Group 14.2.90, holotype QM G300980).

FURTHER RECORDS. Tasmania (Oyster Bay, AM U182).

COLONY. The holotype colony consists of firm, rounded vertical lobes and lamellae up to about 1cm thick, sometimes coalescing with one another along their length. Common cloacal apertures are on the rounded terminal ends of the lobes. A superficial layer of bladder cells overlies a layer of stellate spicules. Sparse spicules also occur amongst the zooids and line the posterior abdominal common cloacal cavity that separates the outer (zooid) layer of the colony from the central test core (where spicules are particularly sparse). The common cloacal cavity also surrounds groups of zooids and penetrates between them at thorax level. The colonies from Tasmania have less rounded and thinner colony branches. However, in their common cloacal systems and in the form and distribution of spicules, they resemble the holotype.

The spicules (to 0.125mm diameter) have 9–11 conical rays in optical transverse section. Ray length/spicule diameter ratio is about 0.25.

In the deck photograph taken before fixation the holotype is a reddish-brown, although the collector's notes record it as light yellow. It was abundant on wharf piles and on mud beneath the wharf.

ZOOIDS. The holotype zooids are about 1.25mm long overall. The branchial siphons are relatively long and cylindrical, about half the length of the thorax. The thorax, oesophageal neck and abdomen are each about the same length. Conspicuous round-tipped columnar epithelial cells project from the body wall. Zooids are difficult to remove from the test. About 6 stigmata are in the anterior rows in the branchial sac but could not be counted accurately. A long retractor muscle projects from about two-thirds of the distance down the oesophagus. The post-pyloric part of the gut loop is bent up against the proximal vertical part. The lens-shaped testis, against the bent-up part of the gut loop, has 7 coils of the vas deferens around it.

In the Tasmanian colonies re-examined in the present study zooids are disintegrated, although they were entire when examined originally by Kott (1962). Their general dimensions are clear from the configuration of the test in the hand cut sections, and, like the holotype zooids, the branchial siphons are long and cylindrical, accommodated in narrow cylindrical channels

through the surface layer of spicules. Testes were not present in the zooids Kott (1962) examined, although well-formed larvae were. The larval trunk is 0.9mm long with 4 ampullae (along each side of the 3 antero-median adhesive organs), ocellus, otolith, and 3 rows of stigmata.

REMARKS. The appearance of the colonies, form of the common cloacal systems and distribution of spicules closely resemble *D. roberti* which, so far, is known only from tropical locations. The present species can be distinguished from *D. roberti* by its narrower colony branches, and shorter conical spicule rays — lacking the attenuated spiky spicule rays of the former species. Zooids are smaller than *D. roberti*, there are fewer stigmata, the retractor separates from nearer the base of the oesophageal neck and there are 7 (rather than 8) coils of the vas deferens. Tropical *D. caesium* and temperate *D. crescente* have similar spicules to the present species but neither has posterior abdominal cloacal cavities. The former species has the same number of vas deferens coils as the present species, but *D. crescente* has more (9). *D. roberti*, *D. fragum* and *D. pecten* have similar cloacal systems to the present species but they do not have such large spicules. *D. microthoracium* has similar sized spicules but they have longer rays and are more crowded, and the common cloacal cavity is thoracic.

Another species with such large spicules, the same number of strong but relatively short conical spicule rays and the same 3-dimensional common cloacal cavity is not known in this genus.

Didemnum tabulatum Sluiter, 1909
(Figs 116A, 167E)

Didemnum tabulatum Sluiter, 1909: 49.

NEW RECORDS. Western Australia (W of Port Hedland, WAM 7.93).

PREVIOUSLY RECORDED. Indonesia (Sluiter, 1909, syntypes ZMA TU480.1–3).

COLONY. The syntypes (ZMA TU480.1–3) have been re-examined. All are robust sheet-like colonies up to 5cm in greatest dimension but only about 2mm thick. One (ZMA TU 480.3) has a featureless surface, although the other two have deep furrows where the surface is depressed over the deep primary canals that surround each group of zooids. Within each group, the cloacal cavity penetrates at thorax level and each thorax crosses the horizontal space associated with an independent ventral strip of test. A thin spicule-free layer of bladder cells is on the surface of the colony. Some dark pigment persists in the surface of the type specimens but was not detected in the newly recorded specimen. Newly recorded colonies, growing over sponges, are white, opaque and thin (to 2.0mm), with a smooth, featureless surface. Thoraces are pale yellow in preservative.

Spicules are sometimes (ZMA TU480.1) sparse and patchy in the surface layer of test, or are evenly spaced and relatively crowded, as they always are in the lower half of the colony where the abdomina are embedded — i.e. beneath the common cloacal spaces. They are up to 0.06mm in diameter, and stellate with numerous (17–19) long, crowded, pointed and almost fusiform rays in optical transverse section. The ray length/spicule diameter ratio is 0.4 or more.

ZOOIDS. Zooids are about 1.0mm long. The oesophageal neck is about one-third of the total zooid length and a long straight retractor muscle projects from it about halfway down. Thoraces are narrow and were too contracted to determine the number of stigmata accurately, although it is not likely that there are more than 6 per row. The post-pyloric part of the gut loop is bent up ventrally and to the right. Gonads were not detected in the newly recorded specimens. Sluiter (1909) reported 5 coils of the vas deferens around the undivided testis, although 7 coils were found on re-examination of one of the syntypes (ZMA TU480.1).

REMARKS. Long, pointed spicule rays are a character of the species. Sluiter's (1909) report of short-rayed spicules probably resulted from problems in interpreting the form of these opaque structures with the light microscope. The spicules resemble *D. lacertosum*, which has a similar number of equally pointed but not such long or crowded rays, a few of them having blunt, rounded tips. *D. astrum* also has crowded pointed conical rays but they are shorter and fewer in optical transverse section. *D. contortum* Monniot, F. & Monniot, C., 1997 has similar spicules, but the colonies are different.

Didemnum ternerratum sp. nov.
(Figs 16B–D, 167C)

Didemnum ternatanum: Kott, 1972b: 179.
Didemnum roberti: Kott, 1976: 68; 1998: 83 (part, Bass Strait and Great Australian Bight records).

TYPE LOCALITY. South Australia (Great Australian Bight, Elliston Bay, coll. S.A. Shepherd et al., May 1971, holotype SAM E2653).

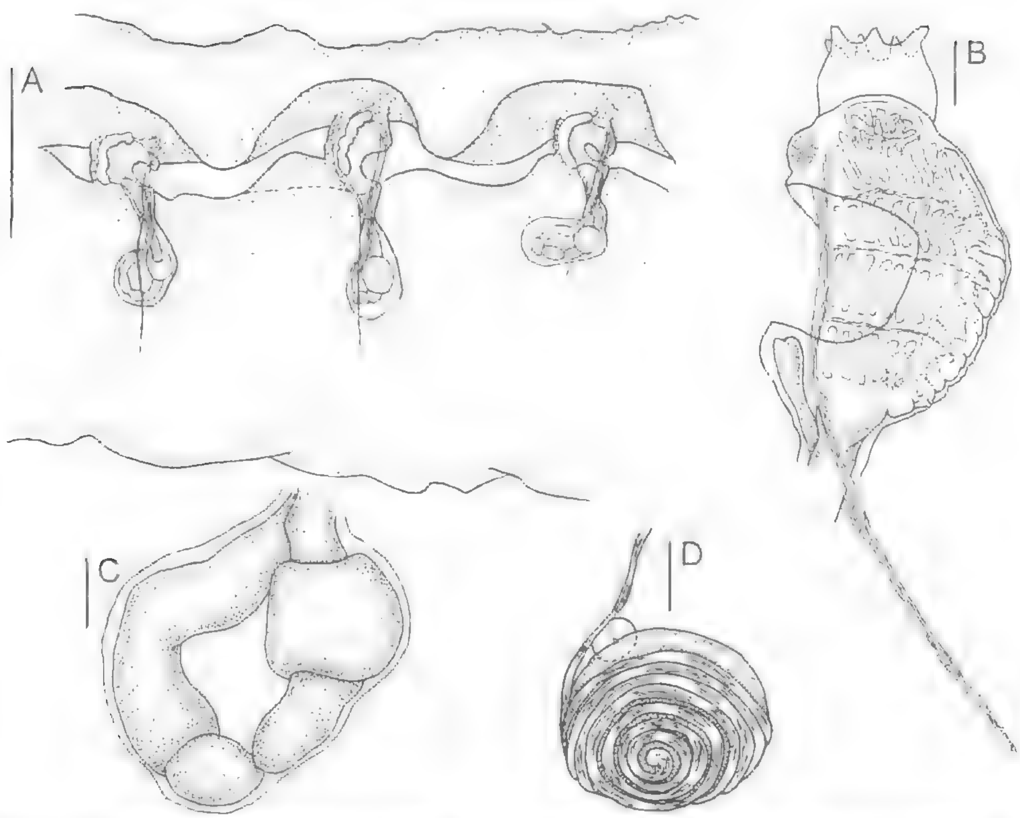


FIG. 116. A, *Didemnum tabulatum* (WAM 7.93) – A, semidiagrammatic vertical section through colony. B–D, *Didemnum ternerratum* sp. nov. (B, SAM E2836; D, MV F68755; C, QM GH930) – B, thorax, faecal pellet being ejected from rectum; C, gut loop; D, testis. Scales: A, 0.5mm; B–D, 0.1mm.

FURTHER RECORDS. South Australia (Wright I. exposed side, SAM E2669; Ward I., QM GH930; Elliston Bay, SAM E2836). Victoria (Western Port – MV F68755, F68805 Kott, 1976).

COLONY. Colonies are thin and hard, packed with spicules throughout, with some ridges and creases on the surface or with the surface raised into domes. They are white in preservative. Branchial apertures sometimes are stellate and outlined in spicules, or they appear in the hard surface as small dimples. A large plug of spicules is in the branchial siphon. A few large closed common cloacal apertures with spicules packed hard around their rims are along the higher parts of the colony or terminal on raised domes. Sometimes they are obscure, and are located only by the absence of branchial apertures around them. Some spicules are globular, with flat-tipped rays and others are stellate, to 0.045mm in diameter with 15–17 short, usually conical but sometimes rounded, rays in optical transverse section. The ray length/spicule diameter ratio is about 0.2.

Primary common cloacal canals surrounding clumps of zooids are deep, extending the full length of the zooids. They penetrate into these clumps at thorax level, and occasionally extend behind the zooids. Generally zooids are crowded in the colony, although sometimes (SAM E2669, QM GH930) thoracic cavities are not developed, and zooids are present only along each side of the deep primary canals with their ventral surfaces embedded in the solid stands of zooid-free test. Colonies are white to brownish in preservative. One colony was reported to be bright orange in life, and the preservative is stained brownish orange (SAM E2836).

ZOOIDS. Zooids are robust being nearly 2mm long, even when the thoraces are contracted, but they are difficult to remove from the hard test. Branchial siphons are moderately long and cylindrical with 6 distinct branchial lobes around the rim. A long atrial lip extends from the upper margin of the wide opening. In the branchial sac 8 stigmata are in the anterior row, reducing to 6

posteriorly. The robust gut forms a vertical loop, and is divided into oesophagus, stomach, duodenum, oval posterior stomach, and large rectum (forming the ascending limb of the loop). A long, strong retractor muscle projects from the upper part of the oesophageal neck. The large hemispherical undivided testis, against the dorsal side of the distal part of the gut loop, has 9 coils of the vas deferens around it. Larvae are not known.

REMARKS. Kott (1962) assigned this species to *D. ternatanum* (<*D. molle*) on the basis of the large common cloacal cavity and the common cloacal apertures on raised parts of the surface. Neither the colonies (which in *D. molle* are vase-shaped, consisting of a single system with a more extensive cloacal system), nor the zooids, resemble the tropical *D. molle* in any way. The present species has large zooids with well formed branchial siphons and atrial tongues, characters shared with the sympatric *D. patulum* from which it is distinguished by its more extensive cloacal cavities and larger spicules with more numerous rays. Also sympatric, *D. jucundum* has similar, though larger and less crowded spicules, and more numerous coils of the vas deferens. Tropical species with similar spicules are *D. lacertosum* (which has more pointed spicule rays and a conspicuous superficial layer of bladder cells) and *D. vahatuio* (with fewer conical spicule rays, some in a polygonal base).

Colonies assigned to *Polysyncraton paradoxum* by Kott (1972b) also were reported to have been bright orange but are distinguished by their single layer of spicules, and less extensive cloacal systems, as well as generic characters.

Didemnum theca sp. nov.
(Figs 117A–C, 167-I)

TYPE LOCALITY. Western Australia (41 n miles WNW of Port Hedland, 36m, coll. J. Marshall on FV Soela 22.8.82, syntypes WAM 121.93).

FURTHER RECORD: ? Western Australia (39 n miles NNE Dampier, WAM 525.92).

COLONY. The syntype colonies are small, firm and rounded, up to about 1cm in greatest dimension. Sometimes they are about the same height, with the basal layer of test thick and projecting up into the centre of the colony. The surface of these hard, white colonies tends to be marked off into circular or oval swellings by creases where the surface test is depressed over the deep primary cloacal canals around each clump of zooids. The clumps are penetrated only by shallow, horizontal thoracic common cloacal spaces, the thoraces crossing the space in separate test sheaths. The surface layer of test, separated by the cloacal cavity from the central or basal test (in which abdomina are embedded), contains the well-formed branchial siphons. Also, there are crowded spicule-filled papillae on the surface. These are especially conspicuous in the depressions over the primary cloacal canals, although it is not impossible that they have been rubbed off on other parts.

Spicules, to 0.07mm in diameter, have rod-like or club-shaped rays, about 11–13 in optical transverse section. The maximum ray length/ spicule diameter ratio is about 0.4 although some spicules have quite stumpy rounded rays.

The irregular specimen from Dampier (WAM 525.92) has spicules like those of the holotype although, apart from patches around each branchial aperture, they are only sparse in the surface and (again unlike the type) the colony has high ridges and folds on the surface.

ZOOIDS. Zooids are about 1.5mm long. The thorax and oesophageal neck are about the same length. The post-pyloric part of the gut loop is bent ventrally at right angles to the longitudinal axis of the zooid. The branchial sac has 11 stigmata per row. The testis is undivided and surrounded by 8 coils of the vas deferens. Larvae are not known.

REMARKS. The relatively large spicules with numerous blunt-tipped rays are similar in size and form to *D. sordidum* but have more rays. The spherical, free black cells characteristic of *D. sordidum* were not detected. Similar spicules also occur in *D. jedanense* and *D. psammatode* but they are smaller and some have more rays. *D. scopi* has similar but smaller spicules with fewer rays. The temperate *D. monile* has similar although softer colonies and also has similar though significantly smaller (maximum diameter about 0.02mm) spicules with the same number of rays.

Didemnum tonga (Herdman, 1886)

Leptoclinum tonga Herdman, 1886: 269.
Not *Didemnum tonga*: Kott & Goodbody, 1982: 520 (< ? *Didemnum membranaceum*).
Didemnum productum Monniot, 1995: 323.

PREVIOUSLY RECORDED. Western Pacific (Friendly Is, Herdman 1886; Marion Reef, Coral Sea, Monniot, 1995). Records are both from about 35m.

COLONY (after Herdman, 1886; Monniot, 1995). Only a single colony is known from each location. They are irregular, encrusting sheets with the surface marked off into a mosaic of polygonal zooid-free areas by depressions over the deep primary circular common cloacal cavities that surround them. Zooids are along each side of the common cloacal canals. Spicules,

crowded throughout the test, are of two sorts. Some spicules (to 0.06mm diameter) have about 9 long, rod like rays in optical transverse section and a ray length/spicule diameter ratio of about 0.4. Others to 0.05mm diameter, have fewer rays — 5–7 conical but rather blunt-tipped rays in optical transverse section — and a ray length/spicule diameter ratio of about 0.35. The Marion Reef specimen was dark violet in life.

ZOOIDS (after Herdman, 1886; Monniot, 1995). Zooids have relatively long cylindrical branchial siphons with inconspicuous branchial lobes. The retractor muscle separates from the lower part of the relatively long oesophageal neck. The branchial sac may have as many as 9 stigmata in the anterior row (Monniot, 1995, fig. 13E). The relatively flat lens-shaped testis is reported (Monniot, 1995) to have 9 coils of the vas deferens around it, although only 7 could be counted in the 2 zooids figured. The large larvae (1.0mm long trunk) in the Marion Reef specimen, are variable, having 4–6 pairs of epidermal ampulla, or an unequal number on each side of the 3 antero-median adhesive organs.

REMARKS. Spicules resemble some in *D. scopi*, having 9–11 long rod-like rays in optical transverse section or fewer, shorter conical rays. The species differ in the form of the systems, *D. tonga* having its zooids arranged along each side of circular canals that surround zooid-free areas of test which appear on the surface as a mosaic of raised areas. *D. elongatum* has a similar long oesophageal neck, but although its spicules are of 2 types and are much the same size as the present species, they have more rays and do not include the ones with rod-like rays found in *D. tonga*.

Didemnum uturoa Monniot & Monniot, 1987
(Figs 117D–F, 165E,F)

Didemnum uturoa Monniot & Monniot, 1987: 43. Monniot, 1995: 329.

NEW RECORDS. Queensland (Capricorn Group, QM G301956, G308107, G308157, G308160, G308176, G308287; Swain Reefs, QM G305804, G308360).

PREVIOUSLY RECORDED. French Polynesia (Monniot & Monniot, 1987). New Caledonia (Monniot, 1995).

Except for the two specimens from the Swain Reefs collected at 20m (QM G305804) and 15m (QM G308360), the newly recorded material is from low tide level on the under surfaces of rubble. The suggestion (Monniot & Monniot, 1987) that *D. uturoa* is only found at depths greater than 15m (as a distinction from *D. digestum*) is not confirmed.

COLONY. Colonies are small cushions to 2cm long with rounded margins or more extensive flat, soft sheets. A thick superficial bladder cell layer is conspicuous around the outer margin, and in preservative it contains brown pigment cells. One lot of small colonies (QM G305804) have chimney-like, raised common cloacal apertures from central common cloacal cavities. Common cloacal apertures are large with white spicules in the rim, the bladder cells being absent. Spicules are crowded through the remainder of the test. The white colour seen through the open, sessile, cloacal apertures results from the crowded spicules in the lower half of the colony (in the floor of the cloacal cavity) contrasting with the brown pigment in the superficial bladder cell layer. Spherical brown pigment cells are often gathered into large, soft, spherical masses in the test.

In life, some colonies are a pale peach colour, although the pigment in irregular cells in the bladder cell layer is dragon's blood red[R], and zooids are yellow. The 2cm long colonies from Swain Reefs (QM G305804) are prune purple[R] and white with prune purple[R] zooids. In preservative their surface test looks wrinkled and spherical vesicles give it a frothy appearance. Here and there, spicules are absent resulting in black flecks where the pigmented test is exposed. Zooids are difficult to remove from the test.

Most spicules are oval to elliptical, the flat-ended rays at opposite ends of the oval being longer than those along the sides. At each end of the oval, many of the spicules have a large, thick terminal, conical ray (to 0.07mm long) changing the outline of the spicule from oval to fusiform. Small oval spicules are up to 0.03mm long, while the fusiform ones with a long conical ray at each end are up to 0.1mm long overall. Sometimes 3 large conical rays are triradially arranged. Spherical burr-like spicules often have numerous rays, but globular spicules with fewer rays occur and oval spicules often have as few as 7 rays around the meridian.

ZOOIDS. Zooids are small, about 1mm long, the thorax and abdomen of about equal length. The branchial siphon is wide and cylindrical, with 6 sharp points around the rim. These are short and stumpy to long, fine tentacular processes about the same length as the rest of the siphon. Their variable length is related to contraction of the fine longitudinal muscle fibres they contain. The siphon is relatively long, its length possibly related to the thickness of the superficial layer of bladder cells which it must pass through to reach the surface. The atrial aperture is a wide opening exposing much of the middle part of the branchial sac to the

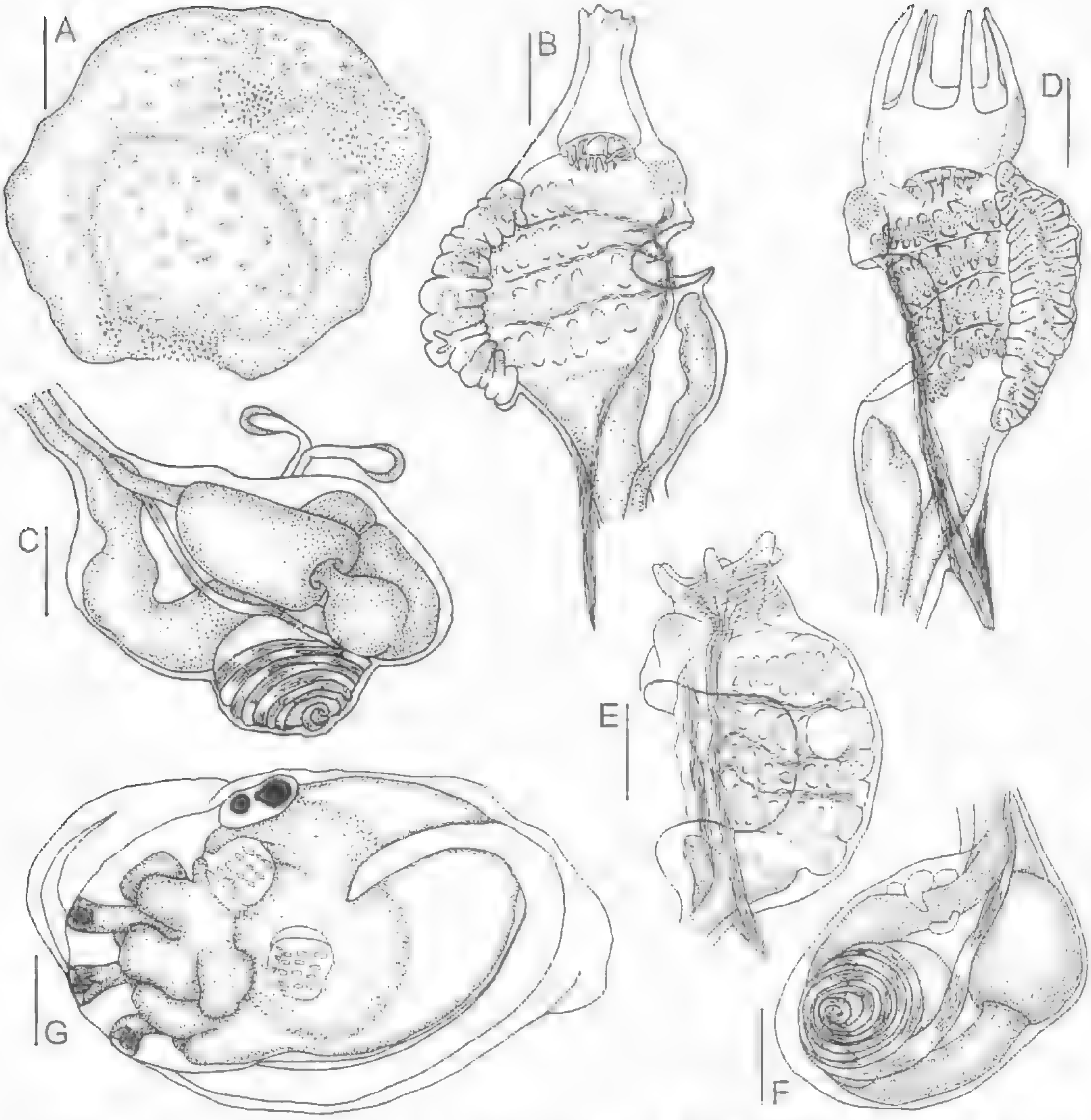


FIG. 117. A–C, *Didemnum theca* sp. nov. (A,C, WAM 121.93; B, WAM 525.92) – A, colony; B, thorax; C, abdomen from right side (WAM 121.93). D–F, *Didemnum uturoa* (D,F, QM G308176, E, QM G308157, G, QM G308160) – thoraces showing D, extended and E, contracted branchial lobes; F, gut loop and bilobed testis; G, larva showing oozooid and thoracic blastozooid. Scales: A, 2mm; B–G, 0.1mm.

cloacal cavity. An atrial tongue is not present. A relatively short retractor muscle projects from a short distance down the oesophagus. In the branchial sac, about 6 stigmata are in the anterior row and 4 in the posterior row although these could not be accurately counted. The gut forms a short rounded loop with the proximal part of the rectum kinked up over the gonads. The testis is subdivided into 2 lobes which together form a low dome with 6 coils of the vas deferens around its outer surface.

Larvae, found in specimens from Heron I. in March (QM G308160, G308176), are being released through the surface. The trunk is 0.45mm long and the tail is wound three quarters of the way around it. Four lateral ampullae are along each side of the 3 median adhesive organs although occasionally one of the ampullae on the left is divided into 2. The usual ocellus and otolith

are in the cerebral vesicle of the oozooid. A thoracic blastozooid is present in the thick larval trunk. Three rows of stigmata are in the oozooid and 4 in the blastozooid.

REMARKS. Apart from *D. chartaceum* (which lacks spicules in the basal test), few *Didemnum* spp. have such a thick superficial layer of bladder cells. The present species resembles *Polysyncraton meandratum* and *P. purou*, both of which have a thick superficial layer of bladder cells. However, both of these lack spicules in the lower half of the colony. *D. fragile* has a bladder cell layer with similar dark pigment, but thinner than in the present species, and its spicules are globular. Spicules of *Lissoclinum calycis*, *L. taratara* and *L. nebulosum* have thick or fused spicule rays drawing out the outline of the spicule to fusiform or diamond shapes as in the present species, although in the *Lissoclinum* spp. many of the spicule rays are needle-like and more numerous. *D. digestum* Sluiter, 1909 from French Polynesia and Fiji (see Kott, 1981; Monniot & Monniot, 1987) has a few enlarged rays on its spicules. However the spicules have fewer rays than the globular and burr-like ones of the present species, and the spicule rays are set in characteristic polygonal concavities in the central mass. Further, the testis of *D. digestum* is not subdivided. None of the other *Didemnum* spp. known to have a subdivided testis (viz. *D. bimasculum*, *D. bisectatum*, *D. recurvatum* and *D. rubeum*) have bilaterally symmetrical spicules. The surface bladder cell layer with its brown pigment, unusual spicules and 2-lobed testis characterise the species.

Didemnum vahatuio Monniot & Monniot, 1987
(Figs 118A, 169A; Pl. 15G)

Didemnum vahatuio Monniot & Monniot,, 1987: 43. Monniot, 1995: 330.

NEW RECORDS. Queensland (Swain Reefs, QM G305373, G305717).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1995). French Polynesia (Monniot & Monniot, 1987).

COLONY. The newly recorded colonies are large, thin, sheets, hard and brittle, with spicules crowded throughout. In life, one colony (QM G305717) had a fairly regular mesh of small oval olive green[R] or drab depressed areas with chocolate[R] zooids separated by narrow chocolate[R] coloured ridges. Another (QM G305373) had a less regular mottled pattern of ecru drab[R] and liver brown[R] with 2mm wide elevated ridges around circular to longitudinal depressions containing liver brown[R] zooids. In preservative both colonies are green, and the preservative is stained green, raised areas are light green to white and depressions are brown to green. Zooids are pale brown-green in preservative. The green colour is not apparently the result of plant cell symbionts, and is collected into reservoirs of greenish black pigment in the basal test of preserved specimens. Zooids are in the slightly depressed areas of test, surrounded by common cloacal spaces. The elevated areas are zooid-free.

Spicules are particularly crowded in the basal part of the colony, which is white, without pigment. Spicules are stellate to 0.07mm diameter with 13–15 well separated, short conical pointed rays in optical section. The conical rays sometimes appear to be set into concavities in the central mass of the spicule.

ZOOIDS. Zooids are small, about 1mm long. Each has a long branchial siphon, with 6 sharp points on the rim of the aperture. The wide sessile atrial aperture exposes most of the branchial sac to the common cloacal cavity. A fine retractor muscle projects from the upper part of the oesophagus. The gut has the usual subdivisions and the distal part of the loop (consisting mainly of the posterior stomach and thick proximal part of the rectum) is flexed ventrally over the testis. The undivided testis is relatively flat, with 6 coils of the vas deferens around it.

Larvae are known only from the French Polynesian and New Caledonian specimens (Monniot & Monniot, 1987; Monniot, 1995) they have a small trunk only 0.28mm long, with 4 pairs of lateral ampullae and the tail wound almost the whole way around it.

REMARKS. The newly recorded colonies are more extensive than those from New Caledonia and French Polynesia and also differ in their green colour. Nevertheless, crowded spicules, their size and form, long branchial siphon, and number of vas deferens coils are the same in all recorded material.

Spicules are a little like the stellate ones of *D. multispirale* with the rays set far apart on the central mass. However, *D. multispirale* also has globular spicules, more spicule rays and more coils of the vas deferens. *D. tabulatum* Sluiter, 1909 has a similar colony but although its spicules are a similar size, they have longer, more crowded rays. Preserved colonies of *D. viride* are the same greenish-white colour in alcohol and have crowded spicules like the present species,

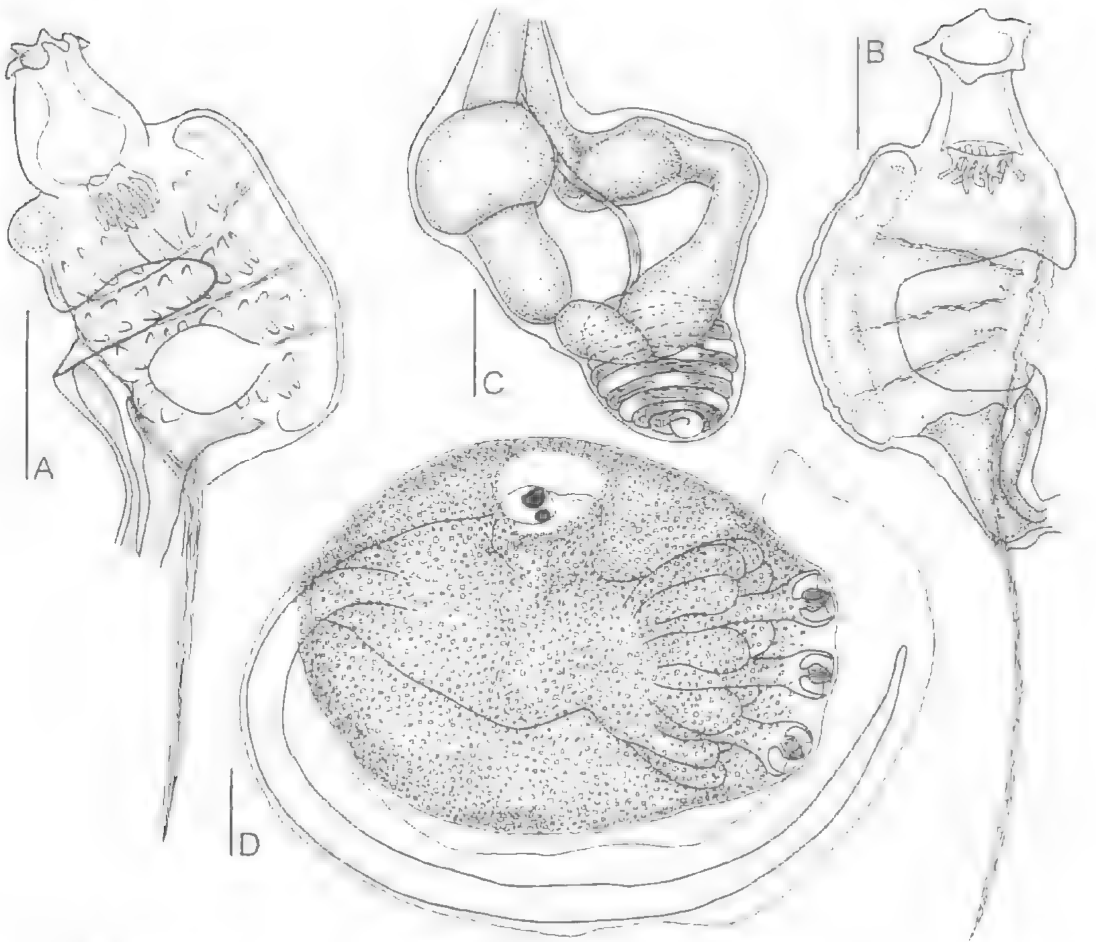


FIG. 118. A, *Didemnum vahatuio* (QM G305373) – A, thorax. B–D, *Didemnum verdantum* sp. nov. (QM GH5358) – B, thorax; C, gut and gonads from ventral surface; D, larva with symbionts embedded in the larval test, absent from windows over cerebral vesicle and adhesive organs. Scales: 0.1mm.

but it does not have the same surface pattern, and its spicules have fewer rays.

Didemnum verdantum sp. nov.
(Figs 118B–D, 171-I; Pl. 15H)

TYPE LOCALITY. Northern Territory (35 n miles W of Bathurst I., 16m, coll. AIMS Bioactivity Group 15.8.87, holotype QM GH5358).

COLONY. The holotype is a thin, dark, encrusting sheet, the dark colour resulting from dark zooids showing through a circular spicule-free thin layer of test that surrounds each branchial aperture. A layer of spicules lines the siphon and spicules line the margin of the stellate aperture. The dark colour is caused by dark spherical cells that lie free in the test around the zooids and in the haemocoel. Colonies are grass-green in life. The common cloacal cavity is horizontal, at thorax level, the thoraces crossing it each with its own ventral test strip. Abdomina are embedded in the basal test, together with the large embryos.

Spicules are crowded throughout the colony, and minute *Prochloron* cells are mixed with them in the surface layer of test. Spicules are to 0.093mm diameter with 5–7 spindly rod-like rays in optical transverse section. Tips of the spicule rays are pointed, rounded or flat. The ray-length/spicule diameter ratio is at least 0.4.

ZOOIDS. Zooids are small with a short branchial siphon, and sessile atrial aperture with the branchial sac exposed directly to the common cloacal cavity. The retractor muscle projects from about halfway down the oesophageal neck.

About 6 stigmata are in the anterior row but these could not be counted accurately. The undivided almost spherical testis with 10 coils of the vas deferens around it lies against the ventrally flexed post-pyloric part of the gut loop

Larvae, in the basal test of the holotype, are large (trunk 0.7mm long) and conspicuous with the tail wound two-thirds of the distance around the trunk. The larval test is thick, and crowded with *Prochloron* cells that make it a fluffy yellowish colour in preservative, and obscure the structure. Embedded *Prochloron* is absent from an oval area in front of the 3 anterior median adhesive organs and a circular area over the cerebral vesicle. A distinct waist separates the anterior adhesive array from the larval oozooid. The former consists of 6 large finger-like ectodermal ampullae along each side of the antero-median adhesive organs. A particularly long lateral horizontal ampulla projects from the waist on the left side of the larval trunk. Dark brown spherical cells that confer the colour to the preserved specimens are in the larval haemocoel. The larvae probably are liberated into the base of the common cloacal cavity.

REMARKS. The species resembles *D. etiolum* in its spicules, their distribution, the dark spherical cells in the larval haemocoel and embedded *Prochloron* in the larval and adult test (absent from windows over the adhesive organs and sense cells). It differs from *D. etiolum* in its sheet-like (rather than minute saucer-shaped) colonies, 10 coils of the vas deferens (rather than 6), a larval trunk almost twice as long, more ectodermal ampullae and larger spicules.

The brown spherical cells free in the test and haemocoel are like those in *D. etiolum*, some *D. viride* and other species (see Glossary, **haemocoel**).

Spicules are similar to, but larger than, those of temperate *D. mantile* (distinguished by its circular depressions over the deep primary cloacal cavities, absence of plant cells and dark test cells and fewer coils of the vas deferens). Spicules also resemble those of *D. clavum*, which lacks the plant cell symbionts and the characteristic dark test cells, and has distinctive spiky giant spicules.

Didemnum via sp. nov.
(Figs 119, 172-I)

TYPE LOCALITY. Queensland (Heron I., Hole in the Wall, 15-20m, coll. D. Parry 8.7.81, holotype QM GH808).

COLONY. The colony is a firm, robust brownish sheet with zooids opening along each side of the depressions over the primary common cloacal canals surrounding stands of test that protrude slightly from the upper surface as circular to oval elevations. Occasionally zooids occur also in these solid test masses with secondary cloacal spaces penetrating amongst the thoraces. A thin surface layer of bladder cells makes the surface smooth and slightly shiny. Brown pigment is in the superficial layer of test and is particularly evident around the common cloacal apertures.

Spicules are crowded throughout the colony. They form a plug in the branchial siphon, but do not outline the apertures. They are stellate, to 0.07mm diameter and have 7–9 long tapered rays in optical transverse section. The ray length/spicule diameter ratio is about 0.33.

ZOOIDS. Zooids have a short branchial siphon. A large sessile atrial aperture across the middle of the dorsum lacks an atrial tongue and has a distinct band of muscles around its rim. The dorsal pharyngeal muscles are well-formed, and fine, but relatively conspicuous longitudinal parietal muscles are diverted around the margin of the atrial siphon. A tapering retractor muscle projects into the test from the top of the oesophageal neck. Nine spindle-shaped stigmata were counted in the anterior row of the branchial sac. The gut forms a rounded loop and the top-shaped undivided testis is against its ventrally flexed post-pyloric part. Eleven tight coils of the vas deferens surround the testis.

Embryos are in the thin basal test. The larval trunk is 0.85mm long, and 4 pairs of club-shaped ectodermal ampullae are along each side of the 3 antero-median adhesive organs. The tail is wound three-quarters of the way around the trunk.

REMARKS. The form of the colony and its spicules resemble *D. crescente* from SE Australia. However, the latter species has a characteristic shelf-like lateral organ, sturdier conical spicule rays, fewer stigmata and fewer coils of the vas deferens. *D. mantile* has similar though smaller spicules with long tapering but fewer rays and it has fewer vas deferens coils.

Didemnum viride (Herdman, 1906)
(Figs 120A–C, 172G)

Leptoclinum viride Herdman, 1906: 340.
Didemnum viride: Vasseur, 1970: 216. Kott, 1980: 4; 1998: 84. Parry, 1984a: 503. Monniot & Monniot, 1987: 45. Monniot, 1995: 330.
Not *Trididemnum viride*: Tokioka, 1967: 87 (<*Trididemnum clinides* Kott, 1977; *T. miniatum*, Kott, 1977; *T. nubilum* Kott, 1980; *T. strigosum* Kott, 1980).
Not *Didemnum viride*: Kott, 1982a:101 (<*D. poecilomorpha* Monniot & Monniot, 1996: 161).

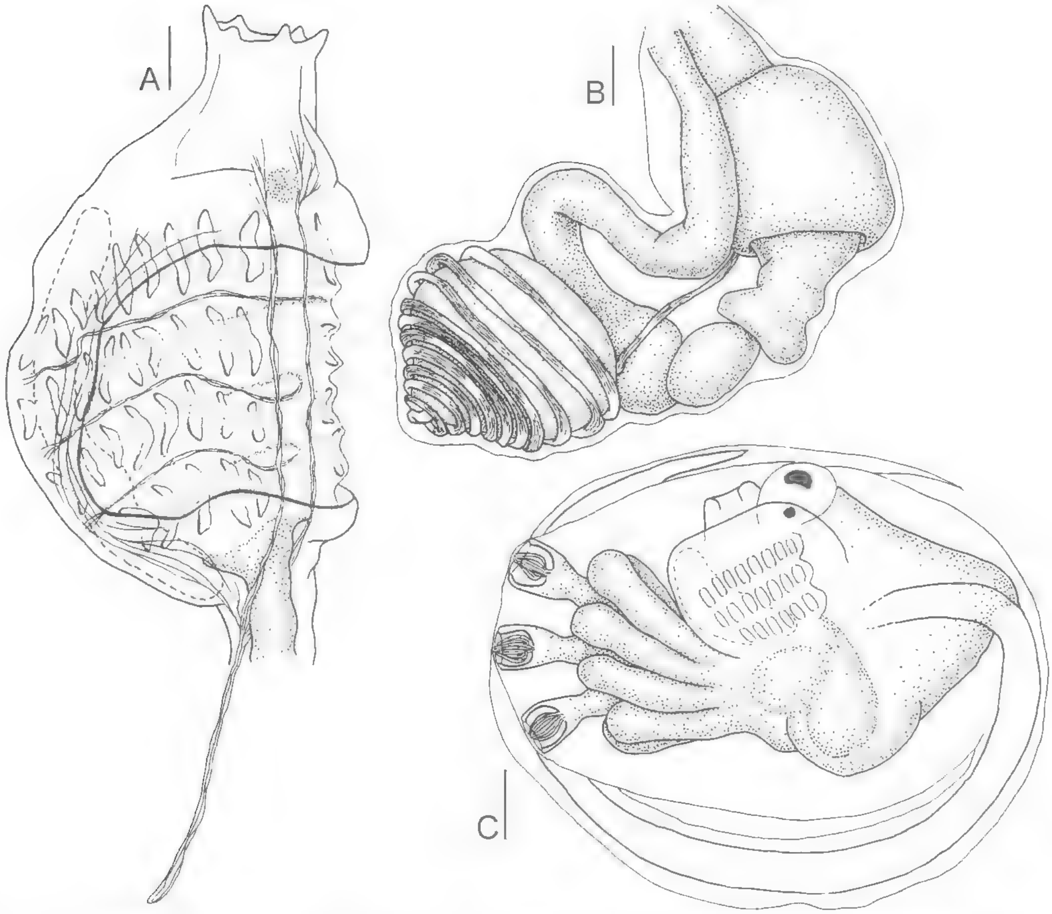


FIG. 119. *Didemnum via* sp. nov. (QM GH808) – A, thorax; B, gut loop and testis from dorsal surface; C, larva. Scales: 0.1mm.

NEW RECORDS. Western Australia (Montebello Is, WAM 921.92). Queensland (Heron I., QM G308013, G308022; Swain Reefs, QM G305798). Papua New Guinea (East New Britain, QM G302890).

PREVIOUSLY RECORDED. Western Pacific (New Caledonia – Monniot, 1995; French Polynesia – Monniot & Monniot, 1987). Indian Ocean (Malagasy – Vasseur, 1970; Sri Lanka – holotype BMNH 07.8.30.41 Herdman, 1906).

COLONY. Newly recorded colonies form encrusting sheets of varying thickness to 1cm. The surface is raised into small rounded prominences separated from one another by narrow, shallow depressions where the surface test is collapsed over the primary common cloacal canals. Zooids open around these prominences, in which the ventral surfaces of the thoraces are embedded but which otherwise usually are zooid-free. Abdomina are embedded in the basal test. Circular common cloacal canals that surround each prominence are usually at thoracic level. In other colonies, zooids are more numerous, the primary cloacal canals are deeper and extend behind a clump of zooids which is anchored to the basal test by a single test connective. Cloacal spaces penetrate around the thoraces in a clump, isolating them from one another, each with its own ventral strip of test. The superficial layer of test contains a mixture of pigment, spicules, prokaryotic algal cells (Cyanophyta) and bladder cells. The remainder of the test contains crowded spicules. Spicules (to 0.045mm in diameter and occasionally to 0.07mm) are conspicuously stellate with 7–9 and sometimes 5 relatively long, conical, but often rather blunt-tipped rays in optical transverse section. Ray length/spicule diameter ratio is about 0.4. Small, crowded, spicule-filled papillae are on some parts of the surface.

Living colonies usually have claret[R] to liver-brown[R] pigment mixed with spicules. Vermilion[R] zooids can be seen through the branchial siphons. Green symbionts are embedded in the whole or part of the superficial test which also has white patches where spicules cluster around the branchial siphons at the surface. In preservative the thoraces are liver brown[R] or reddish-brown[R] sometimes with large brown cells in the haemocoel. The preservative is stained green and oval patches of green Chlorophyta are in the basal test.

ZOOIDS. Zooids are less than 1mm long and sometimes are difficult to remove from the test. The branchial aperture has 6 distinct lobes, and the atrial aperture is a large sessile opening. A circular lateral organ projects from each side of the thorax, and a retractor muscle of variable length projects from the zooid at the posterior end of the thorax. About 8 long stigmata are in the anterior row in the branchial sac. The accumulation of glandular material in the curve of the gut loop is characteristic (Kott, 1980). The gut forms a fairly wide loop, its post-pyloric part flexed ventrally. Gonads are present in French Polynesian and New Caledonian material (Monniot & Monniot, 1987; Monniot, 1995). The ovary is small and an almost spherical testis has 7 coils of the vas deferens around it.

Larvae in the New Caledonian specimens, have a small almost spherical trunk, 0.32mm (Monniot, 1995) long with the tail wound about three quarters of the way around it. The trunk is completely encased in plant cells, except for 'windows' over the sensory vesicle and the adhesive organs. The usual 3 antero-median adhesive organs have 5 pairs of lateral ampullae along each side. A newly recorded specimen (QM G308022) collected from Heron I. in March, has larvae with a 0.45mm long trunk, and the tail wound only halfway around it. Although it was taken from the cloacal cavity it lacks a coat of plant cells. It contains crowded spherical cells in the larval haemocoel and 5 pairs of lateral ampullae.

REMARKS. The species was redescribed (Kott, 1980) from the holotype. It now is known from a wide range in the Indo-West Pacific. Apart from differences in colony size and length of the larval trunk, specimens do not show any great degree of intraspecific variation. Although gonads were not present in the holotype, their presence in subsequent material confirms Kott's generic determination. Colonies from New Caledonia and French Polynesia were not more than 2cm in maximum dimension, contrasting with the extensive sheets (10–12cm) from the Great Barrier Reef. The species is not known from the Philippines or Palau Is. Monniot (1995) overlooked Kott's (1980) re-examination of *Trididemnum viride*: Tokioka, 1967 (USNM 1161, 11640-2, 11646, 11619, 11672, 11680-1, 11796) from the Philippines which Tokioka had assigned to the present species. They are a mixture of *Trididemnum clinides* Kott, 1977, *T. miniatum* Kott, 1977, *T. nubilum* Kott, 1980 and *T. strigosum* Kott, 1980. Subsequently specimens of *D. viride*: Kott, 1982a from the Philippines and Palau Is were also found to be a separate species, *D. poecilomorpha* Monniot & Monniot, 1996. Monniot & Monniot (1996) did not report spicules with flat-and blunt-tipped rays which, together with more (11–13) shorter and more pointed rays of the stellate spicules, larvae with a trunk almost 0.7mm long, and long oesophageal neck, distinguish *D. poecilomorpha* from *D. viride*. *D. herba* from the Great Barrier Reef, with spicules of similar size and with the same number of rays, has shorter and more spiky rays, long branchial siphons and 8 coils of the vas deferens. *D. verdantum*, from the Timor Sea has *Prochloron* rather than Cyanophyta. Its long narrow rod-like spicule rays, large larval trunk (0.7mm) and 10 coils of the vas deferens further distinguish it.

D. vahatuio colonies have a different surface pattern and colour and, although spicules are the same size, they have more rays. *D. guttatum* Monniot & Monniot, 1996, is a similar green colour in preservative, but is distinguished by having more and shorter spicule rays, smaller zooids with 6 (rather than 8) stigmata in the anterior row of the branchial sac, more vas deferens coils and a long branchial siphon.

The present species is one of 8 in *Didemnum* to have obligate symbionts. These are Cyanophyta as in *D. guttatum* and probably *D. herba* and *D. poecilomorpha* rather than *Prochloron* (present in *D. molle*, *D. etiolum*, *D. flavoviride* and *D. verdantum*).

Didemnum vulgare sp. nov.
(Figs 120D-F, 169D)

Didemnum moseleyi: Kott, 1972a: 19 (part, specimen from Goose I.); 1976: 65 (part, specimen from Eagle Rock Western Port).

TYPE LOCALITY. Western Australia (100 n miles SSW Eucla 33°17'S 128°12'E, trawled 175m, coll. W. Zeidler and K. Gowlett Holmes on FV Comet 15.1.89, holotype SAM E2684).

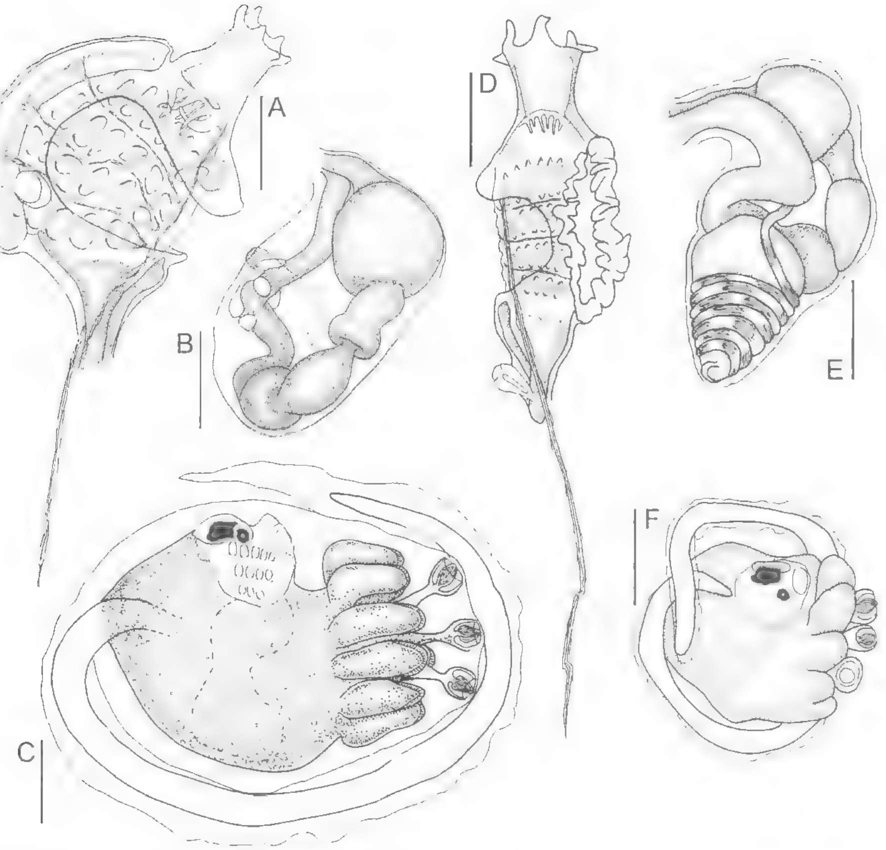


FIG. 120. A–C, *Didemnum viride* sp. nov. (A,B, QM G308013; C, QM G308022) – A, thorax; B, gut loop, dorsal view showing origin of stolonic vessel on ventral side of loop, and vesicles of gastro-intestinal gland; C, larva. D–F, *Didemnum vulgare* (SAM E2684) – D, thorax; E, gut loop and testis; F, larva. Scales: 0.1mm.

FURTHER RECORDS. South Australia (Spencer Gulf, SAM E2849; Rapid Bay, SAM E2837; Kangaroo Is., SAM E2855). Victoria (Western Port–MV F68749, F70201 Kott, 1976).

COLONY. In preservative the holotype is white and opaque, with spicules crowded throughout. Colonies are sheet-like or irregular, and several are on the test of other ascidians (e.g. *Ritterella pedunculata*: MV F70201 and *Herdmania momus*: SAM E2849). An extensive thoracic cloacal cavity has the thoraces crossing it in separate test sheaths. Randomly distributed large, common cloacal apertures are sessile with spicules present in the rims of the openings. Spicules also are crowded in the surface test, continuing without interruption into the branchial siphon linings. SAM E2849 and MV F70201 have 3 or 4 rounded or pointed projections of the spicule-filled, thin surface test around each branchial aperture on some parts of the surface. Sometimes similar papillae are between the branchial apertures (MV F70201). Spicules are stellate, moderate-sized (to 0.06mm diameter), a few with only 9 rays but usually with 11–13 relatively long conical rays in optical transverse section. They break-up readily. The ray length/spicule diameter ratio is 0.3.

SAM E2837 was salmon pink[R] in life.

ZOOIDS. Zooids are small, less than 1mm long. The funnel-shaped branchial siphon is at least one-fifth the length of the rest of the thorax, and has 6 finely pointed lobes around the rim of the aperture. The atrial aperture is a large sessile opening exposing most of the branchial sac directly to the cloacal cavity. Six stigmata are in the anterior row and 5 are in the posterior row in the branchial sac. A long, fine, tapering retractor muscle projects from the anterior part of the oesophageal neck. The gut forms a tight double loop, the distal post-pyloric part bent ventrally against the pyloric part. In the holotype and specimens from Goose I. (SAM E2849) and Western Port (MV F68749, F70201) a conical

testis surrounded by 9 coils of the vas deferens projects behind the ventrally flexed distal part of the gut loop. Small larvae in the basal test of the holotype (January) and MV F70201 (November) from Western Port have the tail wound about one and one-third times around the almost spherical trunk, which is about 0.3mm to 0.4mm long. There is an otolith and ocellus, and 4 rounded epidermal ampullae along each side of the 3 antero-median adhesive organs.

REMARKS. Generally, the present species has no outstanding character, and is distinguished from other similar species on the size and form of its spicules, and its small larval trunk with the tail coiled more than once around it. The southern Australian temperate species, *D. delectum* and *D. macrosiphonium* have smaller spicules and more restricted cloacal systems; *D. lissoclinum* has larger larvae, more extensive cloacal cavities and similar spicules but they have fewer rays; and *D. pellucidum* has similar but much larger spicules, a particularly long branchial siphon and a distinctive colony. The spicules resemble those of tropical *D. membranaceum*, which occurs in South Australia. However, *D. membranaceum* has a larval trunk 0.7mm long, and giant spiky spicules with 4–6 rays.

Kott (1972a) noted that the specimens from Goose I. and some *D. incanum* from Carickalinga Head, differed from *D. moseleyi* in their regularly stellate spicules. Nevertheless, she erroneously assigned them to *D. moseleyi*. She also mis-counted the number of vas deferens coils which, on re-examination are found to have 9 as in the present species (e.g. the holotype and MV F70201).

Genus **Trididemnum** Della Valle, 1881

TYPE SPECIES. *Trididemnum benda* Della Valle, 1881.

Hartmeyer (1909-11) designated *Lissoclinum tenerum* Verrill, 1871 the type species of *Trididemnum*, considering *T. benda* Della Valle, 1881 a nomen nudum. However, as Romanov (1989) correctly asserts, the latter is the type species by monotypy.

Species of this genus have 3 rows of stigmata, an undivided testis, and a coiled vas deferens. Usually, the atrial aperture is on a relatively short, laterally or posteriorly directed siphon, but occasionally (in some algal symbioses) it is a sessile transverse opening exposing the middle of the branchial sac to the cloacal cavity. Spicules usually are stellate with pointed conical rays, although some species have globular or burr-like spicules. They often are large (up to 0.15mm in diameter). Zooids sometimes are relatively large (to 2mm) with up to 15 longitudinal muscles and some transverse ones especially anteriorly and posteriorly in the parietal body wall. Often they have relatively numerous stigmata. However, smaller and more simplified zooids also occur in the genus. Usually a fine retractor muscle projects from the posterior end of the thorax or the oesophageal neck. The gut has the usual divisions of oesophagus, stomach, duodenum, posterior stomach and rectum. Often the posterior stomach increases in diameter to its junction with the rectum (as in *Polysyncraton*), rather than being separated from the rectum by a constriction.

Many species have complex sponge-like colonies in which branches or lobes fold back over the surface or over one another and fuse to enclose spaces or vestibules lined with branchial apertures (see Glossary, **colony shape**).

In one group of species the ectoderm of the body wall usually is black squamous epithelium with pale nuclei, especially around the anterior end of the thorax . The black pigment may fade in preservative, although some may persist longer in the tips of the branchial lobes and in a branchial velum. In a number of species there is an endostylar pigment cap, a cap of pigment in the body wall over the anterior end of the endostyle.

Larvae have the usual 3 antero-median adhesive organs with usually 3–5 but occasionally more (e.g. *T. marmoratum*, *T. nube*, *T. pseudodiplosoma* and *T. spongia*) ectodermal ampullae along each side of the anterior end of the trunk. The ectodermal ampullae sometimes are flattened, with columnar epithelial cells across their tips, and occasionally they are spoon-shaped. Three rows of stigmata are in the larval oozooids (as in *Didemnum*). Unlike *Didemnum* the blastozooids also have 3 rows of stigmata, although, in this genus, larval blastozooids have been recorded only in *T. pseudodiplosoma*, which has up to 7 thoracic and slightly fewer abdominal buds. Adult organs (branchial sac and gut) are well advanced in the larvae. In a well-developed larva a distinct waist separates the adhesive array in the anterior third of the larval trunk from the developing oozooid in the middle to just behind the middle of the trunk. A large spherical yolk mass is in front of the vertical developing gut loop. The posterior end of the larval trunk usually is a pointed cone. The

projecting horizontal ampulla on the left side of the larval trunk from the vicinity of the oesophagus may be obscured by the yolk mass, as it has been observed only in *T. nobile*. Larvae resemble those of *Leptoclinides*, which, however, have 4 rows of stigmata in the oozooid and a vertical yolk mass in front of the gut loop (as opposed to a distinctly spherical one in *Trididemnum*).

Two of the species with black endostylar pigment cap (*T. cyclops* and *T. paracyclops*) and 6 others (*T. clinides*, *T. paraclinides*, *T. strigosum*, *T. nubilum*, *T. dispersum* and *T. miniatum*) are Indo-West Pacific *Trididemnum* species that contain symbiotic algae in apparently obligate symbiosis in the test or in the common cloacal cavity. In most, the algal symbiont is *Prochloron*, which sometimes is present with cyanophytes (*T. miniatum*: Parry, 1984a and Parry & Kott, 1988; and *T. clinides*: Parry, 1984a, Parry & Kott, 1988). *T. dispersum* (>*T. tegulum*) and *T. nubilum* contain only cyanophytes (Kott, 1982a; Kott et.al.,1984; Parry, 1984a; Parry & Kott, 1988). *Prochloron* is the only symbiont to occur in the cloacal cavity (Parry & Kott, 1988). In *T. pigmentatum* non-obligate symbionts are on the surface of the colony. As in *Lissoclinum*, some of the *Trididemnum* spp. in obligate symbioses with *Prochloron* appear to be related (*T. cyclops* and *T. paracyclops*, *T. clinides* and *T. paraclinides*). Taxonomy of the *Prochloron* has not been resolved, so it is not known if the symbionts are the same or related species in each host species (Kott et al., 1984) or each group of host species. Accordingly a symbiosis may have arisen on at least 4 occasions. However they could all have arisen independently on 7 occasions. In the larvae, the plant cells usually envelope the trunk completely, being absent only from clearly defined areas (or windows), one over the cerebral vesicle, and another in front of the adhesive organs. It should be emphasised that these plant cells are not endosymbionts as stated by Monniot (1991). They are in the colony — either in the test or in the cloacal cavity. They are never in the body of the zooids, and they certainly never are intracellular.

Eldredge (1967) discussed 11 species of Indo-west Pacific *Trididemnum* which he divided into the *cerebriforme*, *savignii* and *cyclops* groups based on colony type and zooid form. Within each group, the species appear to have close affinities, and generally the relationships suggested by Eldredge's groupings are confirmed by the dark squamous epithelium in the body wall, presence or absence of the endostylar pigment cap, and presence or absence of an atrial siphon. Within these groups, however, changes with growth from simple to complex folded colonies, variations in and loss of pigment, and variations in distribution of spicules sometimes confuse attempts to resolve species relationships. Nevertheless those characters, together with the size and form of the spicules (albeit not very diverse) and the larvae, appear to comprise the most reliable characters for species identification.

The following 4 species groups each containing species with apparently close affinities, are modified from the groups proposed by Eldredge (1967):

1. The *savignii* group has species with black squamous epithelium especially over the anterior part of the thorax, usually an endostylar pigment cap in the body wall over the anterior end of the endostyle, a posteriorly directed atrial siphon and large stellate spicules (often with long arms). The vas deferens coils about 8 times around the testis and the branchial sac has 10–14 stigmata per row. *T. amiculum*, *T. cerebriforme*, *T. savignii*, *T. areolatum*, *T. natalense*, *T. nobile* and *T. discrepans* have a thick superficial layer of bladder cells and spicules largely confined to a layer beneath the upper surface and one on the base of the colony. *T. vahaereere*, *T. tomarahi*, *T. pigmentatum*, *T. sibogae* and *T. vermiforme* have spicules generally throughout the test and, like *T. amiculum*, *T. cerebriforme* and *T. nobile*, tend to form complex convoluted colonies to 10cm or more. Sometimes *T. nobile* and *T. discrepans* colonies are aspicular. All of these species are reported to have black squamous epithelium and endostylar pigment caps but these are not always present. Their presence or absence could be artefacts of preservation and do not necessarily indicate a genetic difference.

T. crystallinum, *T. lapidosum* and *T. nube* and *T. spongia* from New Caledonia have posteriorly oriented atrial siphons and relatively numerous stigmata and may also be members of this group, but dark squamous epithelium and the endostyar pigment cap are not yet reported for them. All except *T. nube* have complex colonies and *T. spongia* and *T. crystallinum* have a posterior abdominal common cloacal cavity as do other species in the group with complex colonies. As well as these possible members, the group contains *T. amiculum*, *T. areolatum*, *T. caelatum*, *T. discrepans*, *T. natalense*, *T. nobile*, *T.*

pigmentatum, *T. savignii*, *T. sibogae*, *T. tomarahi*, *T. vahaereere*, *T. vermiforme*, and the South African *T. cerebriforme* as well as *T. cerebriforme*: Michaelsen 1924 from New Zealand.

2. The *miniatum* group contains *T. miniatum* and *T. nubilum*, with sessile atrial apertures, algal symbionts and 3 larval adhesive organs but lacking endostylar pigment caps.

3. The *cyclops* group of tropical species form thin encrusting sheets or small lobulating cushions containing *Prochloron* in the common cloacal chamber. The atrial aperture is large and sessile, an endostylar pigment cap is always present and conspicuous. Larvae have only 2 adhesive organs. The group contains *T. cyclops* and *T. paracyclops*.

4. The *dispersum* group contains species with embedded symbionts (*Prochloron* and other cyanophytes). Spicules have relatively short rays and sometimes are globular or burr-like (*T. dispersum*). There is no endostylar pigment cap, and the atrial aperture is on a short posteriorly directed siphon. The members of the group are *T. dispersum*, *T. clinides*, *T. paraclinides*, *T. strigosum*.

Other species do not have obvious affinities within the genus and have not been assigned to a species group.

Superficially, *Trididemnum* may be related most closely to *Didemnum*, which has 3 rows of stigmata in the larval oozooid, a retractor muscle, an undivided testis, a coiled vas deferens and occasionally black squamous epithelium (*D. albopunctatum*). However, many characters are reminiscent of *Leptoclinides*: some (but not all) *Trididemnum* spp. have more stigmata per row than *Didemnum* usually has; a posteriorly directed atrial siphon sometimes has 5 lobes around the aperture (*T. amiculum*, *T. lapidosum*); generally larvae are similar with a distinct waist, limited number (usually 3 or 4) of lateral ectodermal ampullae on each side; and larval blastozooids (except in *T. pseudodiplosoma*) are absent. However, *Leptoclinides* never has a retractor muscle and usually it has numerous male follicles in the testis, 4 rows of stigmata in both zooids and oozoids and the posterior end of the larval trunk is not so narrow and pointed as in most *Trididemnum* spp. Black squamous ectoderm and a retractor muscle occur in *Trididemnum* and in many *Diplosoma* spp. and sometimes in *Lissoclinum* (*L. variabile*) which otherwise have different zooids and larvae from *Trididemnum*. The conspicuous transverse muscles in the parietal thoracic wall of some of the larger zooids are otherwise known only in *Atriolum*.Thus, hypotheses can be developed suggesting a direct relationship between this genus and most other didemnid genera, with the exception of *Polysyncraton*, which it resembles only in the coiled vas deferens. It is not impossible that *Trididemnum*, *Didemnum*, *Lissoclinum* and *Diplosoma* share a common *Leptoclinides* ancestor, and that *Polysyncraton* was isolated independently from *Leptoclinides*.

Trididemnum does not appear to be particularly diverse, only about 30 nominal species being recorded from Australia and the Indo-West Pacific.

KEY TO THE SPECIES OF *TRIDIDEMNUM* RECORDED FROM AUSTRALIAN WATERS

1. Prokaryotic symbionts in common cloacal cavity and/or in test. 17
   Prokaryotic symbionts not in common cloacal cavity or in test 2
2. Black pigment cells in patches or evenly distributed amongst crowded bladder cells 3
   Black pigment cells not amongst crowded bladder cells . 6
3. Spicules in subsurface layer 4
   Spicules not in subsurface layer; or aspicular . . . . *T. discrepans*
4. Spicules to 0.1mm diameter or more 5
   Spicules to 0.05mm diameter . . *T. crystallinum* sp. nov.
5. Spicule rays blunt-tipped. . . . . *T. areolatum*
   Spicule rays sharply pointed . . . . *T. savignii*
6. Posterior abdominal cavities present 7
   Posterior abdominal cavities not present 14
7. Spicules globular and burr-like. 8
   Spicules stellate or aspicular 9
8. Spicules sparse but evenly distributed through colony. *T. spumosum* sp. nov.
   Spicules in single layer in floor of common cloacal cavity . . . . *T. tectum* sp. nov.
9. Branchial siphon more than half the length of the thorax . . . . *T. amiculum* sp. nov.
   Branchial siphon not more than half the length of the thorax 10
10. Spicules with 13-15 rays in optical transverse section; never aspicular . . . . *T. pigmentatum* sp. nov.
    Spicules not more than 13 rays in optical transverse section; sometimes aspicular. 11
11. Colony thin sheet like; not aspicular *T. caelatum* sp. nov.
    Colony not thin, sheet-like; sometimes aspicular . . . 12
12. Vas deferens with 8 coils; spicules to 0.16mm diameter . . . . *T. sibogae*
    Vas deferens with 10 coils; spicules all less than 0.1mm diameter 13
13. Central test core present, surrounded by common cloacal cavity . . . . *T. nobile* sp. nov.
    Central common cloacal cavity, no central test core . . . . *T. vermiforme* sp. nov.

14. Spicules globular and burr-like; or aspicular . . . . *T. pseudodiplosoma*
    Spicules stellate; never aspicular 15
15. Spicules to 0.16mm diameter . . . *T. lapidosum* sp. nov.
    Spicules all less than 0.1mm diameter. 16
16. Spicule rays include comb-, chisel-shaped, sometimes with divided tips . . . . *T. cristatum* sp. nov.
    Spicule rays with pointed tips, never divided . . . . *T. tomarahi*
17. Endostylar pigment cap present; symbionts in cloacal cavity 18
    Endostylar pigment cap not present; symbionts embedded in the test 19
18. Vas deferens coils 10 times . . . . *T. paracyclops*
    Vas deferens coils 6 times . . . . *T. cyclops*
19. Atrial aperture on a siphon 20
    Atrial aperture sessile 22
20. Spicules less than 0.08mm diameter 21
    Spicules to 0.08mm or more diameter . . *T. paraclinides*
21. Colonies with highly arched upper surface; cloacal canals abdominal; stellate spicules with ray length/spicule diameter ratio about 0.2 . . . . *T. dispersum*
    Colonies without highly arched upper surface; cloacal canals thoracic; stellate spicules with ray length/spicule diameter ratio about 0.4 . . . . *T. clinides*
22. Spicules stellate with conical pointed rays . . *T. nubilum*
    Spicules globular with flat-tipped cylindrical rays. . . . . *T. miniatum*

The following species known in adjacent regions are not yet recorded from Australian waters:

Trididemnum cerebriforme Hartmeyer, 1913 from South Africa (see Millar, 1955), forms a complex convoluted colony with 3-dimensional common cloacal systems, a superficial layer of bladder cells, stellate spicules to 0.09mm diameter, small zooids with dark squamous epithelium and an endostylar cap. Although Australian material has been assigned to it, certain characteristics of the colony, zooids and larvae, including spicule distribution, spicule size and form, vas deferens coils, length of the branchial siphon, retractor muscle and number of larval ampullae distinguish the South African species (see *T. sibogae*, *T. nobile* and *T. vermiforme* Remarks, below). *T. cerebriforme*: Michaelsen, 1924 from New Zealand, has a thicker bladder cell layer than either the Australian or the South African material.

Trididemnum fetia Monniot & Monniot, 1987 from French Polynesia, forms thin (1mm) encrusting colonies with a soft but firm test, and rare spicules localised around each branchial aperture. Spicules are to 0.05mm diameter, most with long and only slightly tapered rod-like rays, although some smaller ones have irregular conical rays. Larvae are small (trunk 0.35mm long) with 4 pairs of ectodermal ampullae and 3 adhesive organs. The vas deferens coils 7 times around the undivided testis and an endostylar pigment cap and atrial siphon are present.

Trididemnum granosum Sluiter, 1909 from Indonesia forms small (about 0.5cm) spherical colonies with numerous pointed papillae on the upper (convex) surface. Stellate spicules to 0.027mm diameter with 7–9 rays in optical transverse section are in the superficial layer of test. The species is distinguished by its small colonies and small, stellate spicules with relatively few rays.

Trididemnum marmoratum (Sluiter, 1909) from Indonesia (> *Leptoclinum marmoratum*: see Monniot, 1994: 10) has a posteriorly directed atrial siphon, 3 rows of stigmata with 10 per row, and 6 coils of the vas deferens around an undivided testis. Three antero-median adhesive organs and a circle of lateral ampulla are in the larval trunk. Its affinities have not been determined.

Trididemnum natalense Michaelsen, 1920 has a smooth investing colony, with a thick superficial layer of bladder cells containing pigment and a layer of stellate spicules (to 0.06mm in diameter with 12 rays in optical transverse section) principally beneath the cloacal canals, at oesophageal level. Eight coils of the vas deferens surround the undivided testis, and 8–10 stigmata are in each row. Its differences from *T. savignii* are the spicule layer beneath the cloacal cavity (as in *T. areolatum*) rather than above it (as in *T. savignii*); and the relatively small diameter (0.06mm) spicules which also distinguish it from *T. areolatum*.

Trididemnum nube Monniot, 1991 from New Caledonia has small, translucent encrusting colonies to 6mm thick. Zooids are in oval groups surrounded at oesophageal level by large (0.08mm diameter) stellate spicules with 9–11 pointed rays in optical transverse section. The spicules resemble those of *T. savignii* although the rays are more numerous, not so pointed and the spicules more patchy in their distribution. The zooids have a retractor muscle from halfway down the oesophageal neck. The species is distinguished from others with a single layer of spicules by the oesophageal level of that layer, the large numbers (12 pairs) of larval ampullae, the size of the larval trunk (2mm), a particularly large number (18) of stigmata in each row and isolated oval groups of zooids (like *T. crystallinum*). Although Monniot (1991) referred to the absence of the blastozooids in the context of species differences, this does not constitute a distinction from other known *Trididemnum* spp. as only *T. pseudodiplosoma* from South Australia is known to have blastozooids.

Trididemnum planum Sluiter, 1909 from Indonesia forms smooth, irregular, thin sheets to 10cm, with dark brown pigment in the thick spicule-free superficial bladder cell layer. Spicules are in a crowded layer at thorax level, and a layer beneath the thoracic common cloacal canals. Spicules to 0.06mm diameter have 13 –15 short conical rays in optical transverse section. The small zooids have black squamous epithelium and an endostylar pigment cap, the short, cylindrical branchial siphons open along each side of the common cloacal canals. Short atrial siphons with smooth rounded apertures are on the anterior third of the dorsal mid-line. Recently collected specimens from Darwin Harbour (NTM E191-2: September 1999) conform with Sluiter's (1909) account of the type specimens except for 8 coils of the vas deferens (rather than 6). Larvae, in the basal test of the Darwin specimens, have 5 pairs of slender ectodermal ampullae surrounding the 3 antero-median adhesive organs and the tail wound halfway

around the 1.0mm long trunk. Crowded bladder cells are in the larval test. The species is distinguished from *T. areolatum* (which also lacks spicules in surface and basal parts of the colony) by its relatively small spicules with short and numerous conical rays, its thoracic common cloacal cavity, anterior atrial siphon, black squamous epithelium and endostylar pigment cap.

Trididemnum polyorchis Monniot & Monniot, 1996 has hard pinkish-brown and cream rounded colonies and stellate spicules, to 0.05mm diameter with 9–11 short conical rays. The species is distinguished by its small zooids surrounding small common cloacal chambers, sessile, open common cloacal apertures, the testis divided into 2 or 3 follicles and 4 loose coils of the vas deferens. Zooids have characters that resemble *Polysyncraton* and it is possible that the species has an affinity with that genus rather than *Trididemnum*, which is not otherwise known to have a divided testis or loose vas deferens coils.

Trididemnum spongia Monniot, 1991 from New Caledonia, forms irregular, often massive colonies, with rounded surface elevations and internal sponge-like cavities. Spicules are an averge of 0.07mm diameter with about 11 acutely pointed conical rays in optical transverse section crowded throughout. Atrial siphons are posteriorly oriented. The larval trunk, to 0.9mm long, has 6 epidermal ampullae per side. The species is distinguished from *T. sibogae* by its red zooids, relatively large larval trunk and more numerous larval ectodermal ampullae.

Trididemnum strigosum Kott, 1980 from the Philippines, French Polynesia and Fiji (Kott, 1980, 1982a; Monniot & Monniot, 1987) has thin irregular colonies to 2cm long. Spicules are to 0.08mm diameter, with 7–9 conical rays in optical transverse section and are crowded throughout the colony. Plant cells, as in *T. dispersum*, *T. clinides*, *T. paraclinides*, *T. nubilum* and *T. miniatum* are embedded in the test, mainly above the spicules. Amongst species with embedded symbionts, *T. strigosum* resembles *T. nubilum* and *T. miniatum* in not having an atrial siphon (although a siphon is in *T. dispersum*, *T. clinides* and *T. paraclinides* and most other species of the genus). Spicules are similar to those of *T. paraclinides* but they are smaller, and more crowded. The larval trunk is only 0.7mm long and has plant cells embedded in the test all around the trunk, leaving windows over the adhesive organs and sensory vesicle as in *T.clinides* and *T. miniatum*. The latter species has smaller spicules to a maximum of 0.06mm in diameter, and they are never crowded throughout the colony. *T. nubilum* also has small (to 0.04mm diameter) spicules that distinguish it from *T. strigosum*.

Trididemnum vahaereere Monniot & Monniot, 1987 from French Polynesia, resembles the sympatric *T. tomahari* and *T. pigmentatum*. The latter species has larger spicules with more numerous and longer rays. *T. vahaereere* is distinguished from *T. tomahari* by the origin of the retractor muscle from the base, rather than the top, of the oesophageal neck, and by the 3 rather than 4 ectodermal ampullae on each side of the larval trunk. *T. strigosum* has dark pigment around the branchial siphon but differs in the absence of an atrial siphon and in the symbionts in the test. *T. fetia* has similar colonies and atrial siphons but different spicules.

Trididemnum amiculum sp. nov.
(Figs 121, 174G)

TYPE LOCALITY. Tasmania (39km NNE Devonport, 40°49.8'S 146°31.3'E 68m, coll. Gomon, Poore and Lu, FRV HaiKung Cruise 81-HK-1 04.02.81, holotype MV F70259).

FURTHER RECORDS. NSW (E of Coogee, 5-6mls, sandy substrate, F.R.V. Thetis Statn 44, 15.3.1898, AM Z1681).

COLONY. The holotype is a fragment of a larger colony. It consists of several long, vertical, irregular, cylinders to 4cm long and about 1cm in diameter, each narrowing to a terminal common cloacal aperture and joined to one another along about two-thirds of their length by a flat sheet-like expanse of the colony. The specimen (in preservative) is very hard. Each of the cylindrical lobes contains a central test core, and test connectives cross the common cloacal cavity that surrounds the central core, joining it to the surface zooid-bearing layer of test. Narrow oesophageal secondary cloacal canals penetrate the zooid-bearing layer. Spicules are in a layer in the surface test and in the layer of test surrounding the cloacal cavities. Only sparse spicules are in the central core. The *Thetis* colony (AM Z1681) is a sheet-like investing colony with a smooth upper surface. The surface is raised into vertical lobes with terminal common cloacal apertures and the basal test extends up into the cental cores of the vertical lobes. The distribution of spicules is similar to the holotype with a basal layer and a thick surface layer of particularly crowded spicules (penetrated by the very long branchial siphons) but sparse elsewhere. The posterior abdominal common cloacal cavity is extensive.

Spicules are stellate, to 0.1mm diameter, with relatively short conical rays, 9-11 in optical transverse section. The ray length/spicule diameter ratio is 0.2.

ZOOIDS. The test is tough and the crowded, parallel zooids are almost impossible to remove from it. They are almost 2mm long, narrow and stretched between the surface and the central test, across the common cloacal cavity. The branchial siphon, branchial sac and abdomen (including the mature testis) are each about one-third of the length. The branchial siphon sometimes has a slightly bulbous expansion at its tip. Five small pointed lobes surround the atrial aperture which is on a short posteriorly oriented siphon. A long,

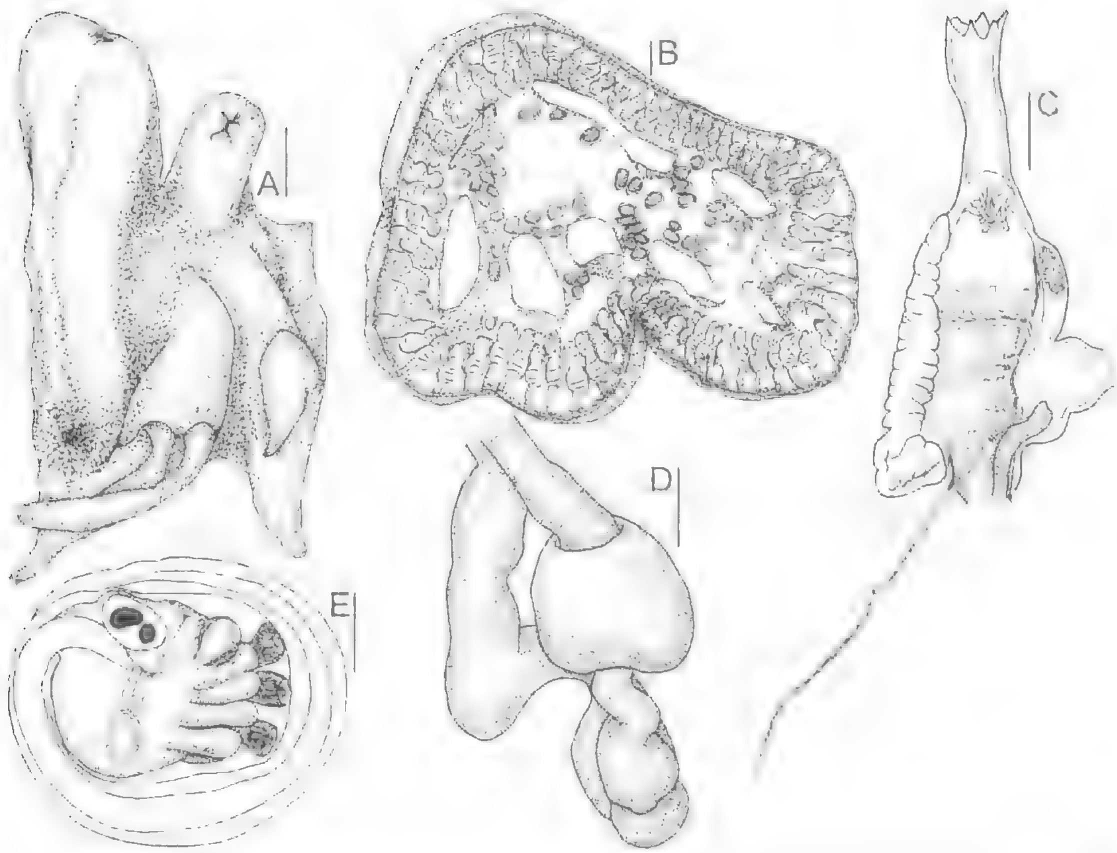


FIG. 121. *Trididemnum amiculum* sp. nov. (A,B,E, MV F70259; C,D, AM Z1681) – A, colony; B, semidiagrammatic transverse section through colony lobe showing zooids at surface, posterior abdominal cloacal cavities and embryos in central test core; C, thorax; D, abdomen; E, larva. Scales: A, 1.0cm; B, 1.0mm; E, 0.1mm.

line retractor muscle projects down toward the centre of the colony, or into the basal test (AM Z1681) from the top of the oesophagus. The gut is a long, narrow vertical loop with the undivided testis against the dorsal surface of the distal part of the loop. Five coils of the vas deferens surround the testis.

Relatively small embryos are crowded in the test connectives and in the basal test of the holotype. They move up toward the common cloacal cavity as they mature, being liberated into the cloacal cavity for release from the colony. Larvae have 5 pairs of lateral ampullae and 3 antero-median adhesive organs. An ocellus and an otolith are present, and the tail winds completely around the trunk, which is only about 0.45mm long.

REMARKS. Although the holotype resembles some less convoluted colonies of the South African *T. cerebriforme* and the tropical *T. sibogae*, and has similar large stellate spicules and 3-dimensional cloacal systems. *T. cerebriforme* has a similar spicule distribution, spicules becoming sparse in the central test, and *T. sibogae* has a variable distribution of spicules — from even distribution throughout to almost aspicular. However, in the present species, spicule rays are shorter, branchial siphons longer, and the relatively small larval trunk has more lateral ampullae. The long branchial siphon of the present species resembles that of *Didemnum elongatum*, although the latter species has a crowded layer of spicules in the middle of the colony rather than in the surface.

The oesophageal neck is longer in the holotype than in the sheet-like colony, and this may be a variable character, changing with growth.

Tridideminum areolatum (Herdman, 1906)
(Figs 122A,B, 173-I; Pl. 16A)

Didemnum areolatum Herdman, 1906: 337.
Trididemnum savignii: Hastings, 1931: 91. Kott, 1981: 184.
Trididemnum natalense: Hastings, 1931: 92. Kott, 1962: 276 (part, pigmented Bargara colony).
Trididemnum banneri Eldredge, 1967: 177. Monniot & Monniot, 1987: 17. Monniot, 1991: 518.

NEW RECORDS. Queensland (Hervey Bay, QM G9447; Heron I., QM G301583, G301601, G301957, G302108, G302306, G308010; Lizard I, QM G302032; Swain Reefs, QM G308426).

PREVIOUSLY RECORDED. Queensland (Bowen – Kott, 1962; Low Is – Hastings, 1931). Central Pacific (Kure and Line Is – Eldredge, 1967; French Polynesia – Monniot & Monniot, 1987). Western Pacific (New Caledonia – Monniot, 1991). Sri Lanka (Herdman, 1906).

COLONY. Colonies are thick (to 3.5cm), firm, cushions to extensive sheets with a smooth surface, rounded margins and irregular outline. The superficial layer of test has bladder cells mixed with black stellate to fusiform pigment cells, sometimes with some spicules. Spicules are mainly crowded in a horizontal layer around the zooids and beneath the oesophageal and deeper abdominal cloacal cavities where they are visible through the common cloacal apertures. Spicules are absent from the lower half of the colony except for a sparse layer on the base. In life, colonies are black, or grey if there are some patches of spicules mixed with the bladder cell layer. In preservative they are grey-brown to brown. Large lacunae of dark pigment are in the basal test. The common cloacal canals are at oesophageal level or sometimes abdominal, but seldom posterior-abdominal.

Spicules are large, often to 0.1mm, and sometimes up to 0.15mm in diameter. They are stellate, with 13–15 blunt conical rays in optical transverse section. Ray length/spicule diameter ratio is 0.25. Crowded between the existing conical rays on these stellate spicules are flat bases of broken rays.

ZOOIDS. Zooids are up to 2mm long, with the thorax, oesophageal neck and abdomen all about one-third of the length. The branchial siphon is long, penetrating the deep bladder cell layer and has 6 long, pointed lobes around the aperture. The atrial siphon, directed posteriorly from the posterior third of the thorax, sometimes has a serrated rim. A fine tapering to short and thick retractor muscle projects from the posterior end of the thorax. A circular lateral organ is on each side toward the posterior third of the thorax. The endostylar pigment cap is often obscured by the dark squamous epithelium of the thorax and abdomen. Longitudinal muscle bands (about 15) are in the thoracic parietal wall. Eight to 10 stigmata are in each row in the branchial sac.

The gut loop is long and open. The duodenum is long and wide, the short oval posterior stomach is in the pole of the loop, and opens into the wide proximal part of the rectum. A narrow constriction surrounded by tubules of the gastric gland separates the proximal third from the distal two-thirds of the rectum. The testis is against the dorsal side of the gut loop and 8 coils of the vas deferens surround it.

Larvae are in the surface test of a colony from Heron I. collected in March (QM G308010). The trunk is 0.8mm long. The tail is short and thick, wound only about halfway around it. The 3 ectodermal ampullae each side of the 3 antero-median adhesive organs are long, slender, spatulate and bent back at the tip.

REMARKS. The principal characteristics of this species are its gelatinous, firm and rather thick colony (to 5mm), with bladder cells in the surface and base, pigment cells mixed with them in the surface, and large spicules with relatively short blunt conical rays in a horizontal layer beneath the bladder cell layer and in the floor of the common cloacal chamber. Zooids have dark squamous epithelium on the body wall, and an endostylar pigment cap is on the anterior end of the endostyle although often it is obscured by the dark pigment in the body wall of the zooid. The 8 coils of the vas deferens and 10–13 stigmata per row were recorded for *T. banneri* Eldredge, 1967 and for the type specimen of *T. areolatum* (Hastings, 1931). The endostylar pigment cap is the only character that was not recorded for these synonyms. Some of the characters observed in the newly recorded specimens, including the blunt-tipped spicule rays and the slender-stalked ectodermal ampullae on each side of the larval trunk are reported for *T. banneri*: Monniot & Monniot (1987). However, Monniot & Monniot (1987) found some variation in the numbers (2–4 per side) of larval ampullae and the larvae (0.6–0.7mm trunk) from French Polynesia were smaller than others assigned to this species. Larvae from New Caledonia are not described.

T. banneri was erected because the type specimens are different from *T. savignii*: Tokioka, 1953. However Eldredge (1967) was wrong in his assumption that Tokioka's (1953) material is conspecific with *T. savignii* (Herdman, 1886). *T. areolatum* was not considered in this context, despite Hasting's

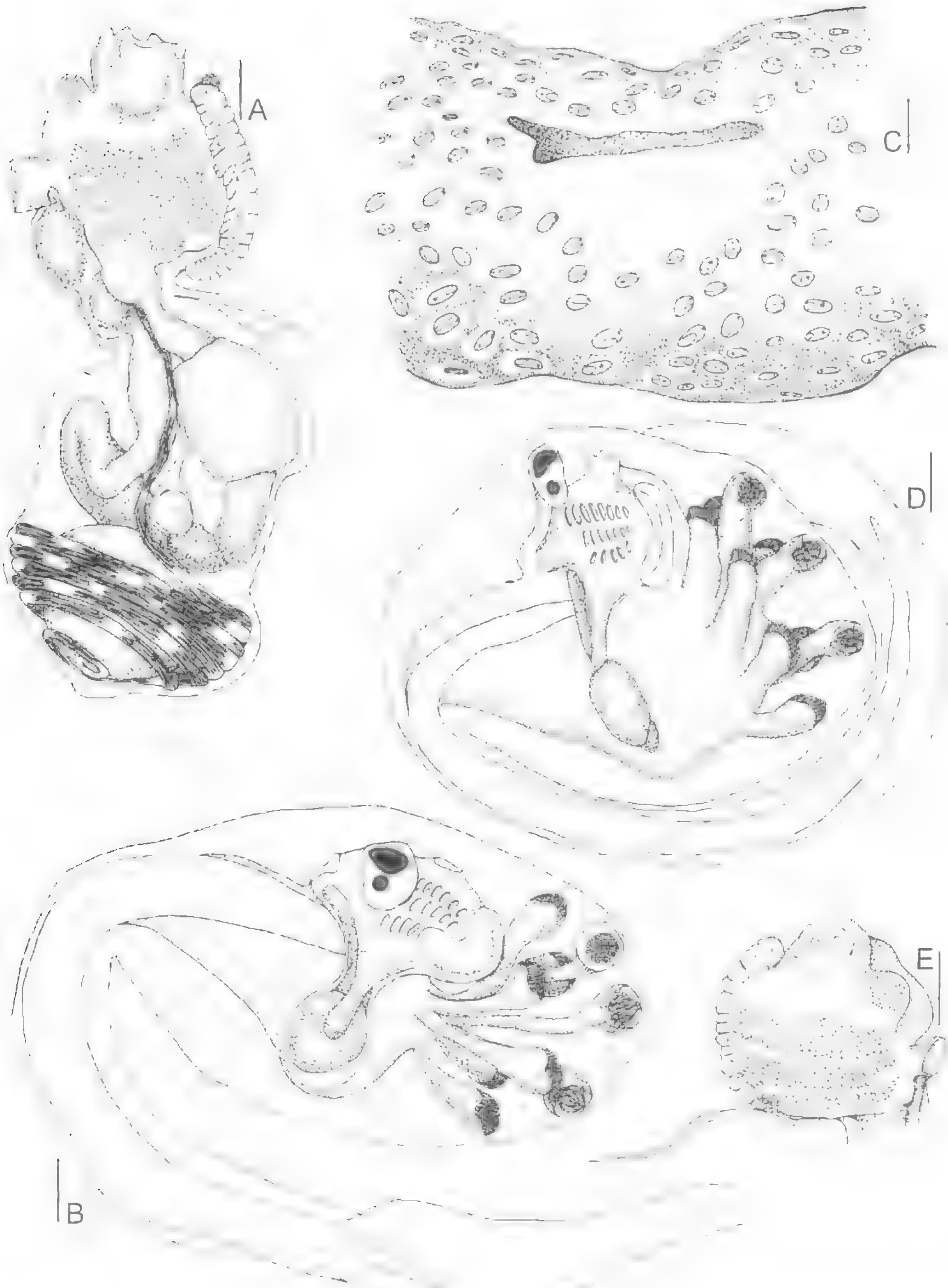


FIG. 122. A, B, *Trididemnum areolatum* (A, QM G308426; B, QM G308010) – A, zooid showing endostylar pigment cap; B, larva. C–E, *Trididemnum caelatum* sp. nov. (SAM E2670) – C, part of colony showing common cloacal aperture and zooids; D, thorax, contracted; E, larva. Scales: A,B,D,E, 0.1mm; C, 1.0mm.

(1931) redescription of the type. Like *T. savignii*, *T. areolatum* has a thick surface layer of bladder cells mixed with dark pigment cells and although its spicules are a similar size to those of the former species, they do not have such sharply pointed rays and are found further away from the upper surface — nearer the middle of the colony. *T. nobile* has similar but smaller spicules, becoming more sparse internally, and its convoluted colonies are different.

T. planum Sluiter, 1909 from Indonesia and Darwin Harbour has some characters of the present species including the layer of spicules at oesophageal level, the surface bladder cell layer, and the blunt-tipped rays of the stellate spicules, but its spicules are only to 0.06mm diameter. *T. planum*: Millar, 1963 from Queensland appears to be incorrectly assigned (see *T. tomarahi*).

T. polyorchis Monniot & Monniot, 1996 from the Palau Is has spicules to 0.05mm diameter crowded throughout, a wide, sessile atrial opening and 3 testis follicles that distinguish it.

Trididemnum caelatum sp. nov.
(Figs 122C-E, 175F)

TYPE LOCALITY. South Australia (Great Australian Bight, SW Eucla, coll. K. Gowlett Holmes, W. Zeidler 14.1.89, holotype SAM E2670).

COLONY. The colony is thin, growing around a weed stalk and other rubble. It has a pitted or embossed appearance owing to the absence of spicules in the test over and surrounding the thoraces so that each thorax appears to be in a concavity in the surface. The surface test is thin, and thin vertical partitions are between the thoraces. Spicules are absent also from large areas of test around each common cloacal aperture. They are in a more continuous layer at oesophageal level and are evenly distributed in the basal test, beneath the posterior abdominal cloacal cavity.

Spicules are large, to 0.1mm in diameter, with 11–13 relatively long, tapering, conical rays in optical transverse section. The ray length/spicule diameter ratio is 0.3. The cloacal cavity is vast and posterior abdominal, crossed only by occasional connectives joining surface to basal test. It effectively divides the colony horizontally into the upper zooid-bearing half and the basal half which is free of zooids but contains the large developing embryos.

ZOOIDS. Zooids are small, and particularly contracted in the holotype. The branchial siphon is short with its rim divided into 6 triangular lobes. The atrial siphon is posteriorly directed from the posterior half of the dorsum of the thorax. A fine retractor muscle projects from the posterior end of the contracted thorax. About 7 stigmata are in the anterior row of the branchial sac, but the thoraces are too contracted for an accurate count. The gut loop is small and rounded, but gonads were not detected.

Larvae are present in the basal test. The larval trunk is large (about 1mm long), particularly deep and almost spherical. The oozooid is halfway along the trunk, occupying its full depth. It has well-developed larval and adult organs. A large sensory vesicle protrudes from the upper surface of the oozooid. Three pairs of rounded ectodermal ampullae are along each side of the 3 antero-median adhesive organs, which have short thick stalks, and there is a median ventral ectodermal ampulla. The branchial sac, has 3 rows of short stigmata across it (about halfway down) leaving extensive unperforated strips of pharynx anterior and posterior to the stigmata. The gut is well-developed, its subdivisions well defined. The tail winds only about halfway around the larval trunk.

REMARKS. Spicule arrangement and the vast posterior abdominal cavity are unusual characters in a thin sheet-like colony. The species resembles some of the more gelatinous colonies of *T. nobile* in the unusual distribution of its spicules. However, the present species has spicules with larger and more numerous and more sharply pointed rays, its colonies are not so complex and its zooids are smaller. *T. pigmentatum* has similar spicules of a similar size, but they are crowded throughout the test. The species is unusual in not having an endostylar pigment cap but it is not impossible that this has faded in preservative.

Although the gonads are not developed, and the number of rows of stigmata in these contracted zooids could not be determined 3 rows of stigmata in the larvae, and a retractor muscle together with a posteriorly oriented atrial siphon indicates *Trididemnum*.

Trididemnum clinides Kott, 1977
(Figs 123A,B, 173H)

Trididemnum clinides Kott, 1977: 617; 1980: 5; 1981; 186 (part, not specimens from Mambualau and Dravuni < *T. paraclinides*); 1982a: 109; 1984: 519; 1998: 91. Monniot & Monniot, 1987: 18. Parry & Kott, 1988: 151.
Trididemnum viride: Tokioka, 1967: 87 (part, zooids with atrial siphons).
Trididemnum sp. Eldredge, 1967: 184.

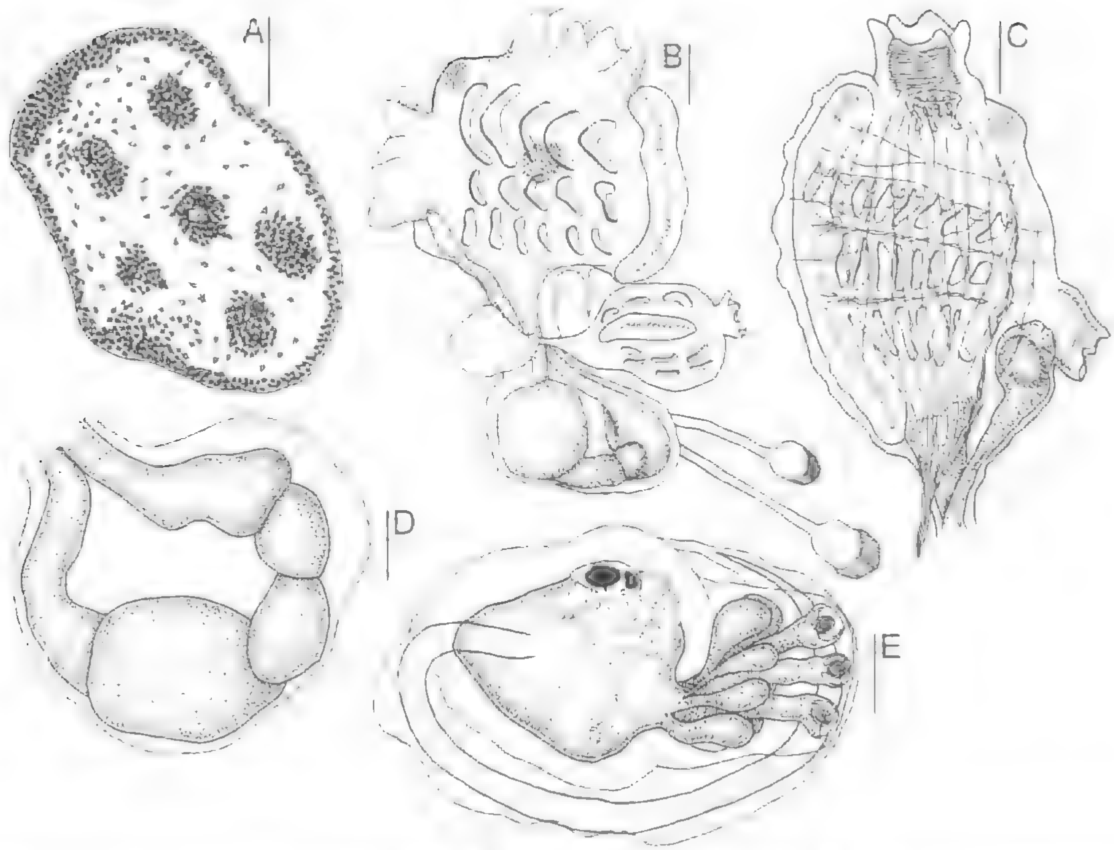


FIG. 123. A, B, *Trididemnum clinides* (after Kott, 1980. QM G12620). A, colony; B, zooid. C – E, *Trididemnum cristatum* sp. nov. (C,D, MV F70208; E, AM Y2321)–C, thorax; D, gut loop; E, larva. Scales: A, 0.5mm; B. 0.1mm.

NEW RECORDS. Queensland (Heron I., QM G301600, G302124).

PREVIOUSLY RECORDED. Queensland (Heron I. – Kott, 1977, 1984). Philippines (USNM 11646 Tokioka, 1967; Kott, 1982a). Fiji (QM G12620 – Kott, 1980, 1981). Guam (Kott, 1982a). Eniwetak (Eldredge, 1967). French Polynesia (Monniot & Monniot, 1987).

The species occupies cryptic habitats near the reef edge.

COLONY. Colonies are small, almost spherical or oval, cushions to 2cm long. Larger colonies are flattened on the upper surface. Each usually contains a single system of zooids, with branchial apertures around a large central horizontal, thoracic, common cloacal cavity, with the common cloacal aperture more or less in the centre of the upper surface. They are fixed firmly to the substrate and often are difficult to remove from it entire. The test is soft. A thin layer of bladder cells is superficial. Spicules sometimes are crowded in the margins and base of the colony, but are sparse in the upper surface except where they are crowded in a patch over each zooid. Each branchial aperture opens near the outer margin of each of these patches of spicules. Small clumps of spicules surround the atrial openings into the cloacal cavity. Elsewhere throughout the colony spicules are evenly but sparsely distributed. Spicules are stellate to 0.04mm in diameter, some with round-tipped cylindrical and others with pointed conical or fusiform rays, 7–11 in optical transverse section. Occasionally the conical tip of a ray is supported in a wider basal section. Except for some spicules with shorter conical rays, the rays are relatively long, ray length/spicule diameter ratio being about 0.4.

Prochloron, a red unicellular cyanophyte and a chlorophyte species (Kott, 1982; Parry & Kott, 1988) are embedded throughout the test, but are most crowded in the surface. The mixture of spicules and green plant symbionts in the test contribute to the cloudy mustard-green colour of these soft colonies.

ZOOIDS. Zooids are about 1mm long, with a wide branchial siphon, its rim divided into 6 deep, pointed lobes. About 5 stigmata are in each of the 3 rows. A circular lateral organ is each side of the thorax between the first and second rows of stigmata. The atrial siphon is short and wide, trumpet-shaped, or often frilled, and projects laterally from the middle of the thorax. A short retractor muscle projects from the posterior end of the thorax near the base of the endostyle. The abdomen is small, with a relatively short oesophageal neck and a short gut loop. Long vascular stolons with spherical terminal ampullae extend into the test from the body wall in the ventral concavity of the gut loop. A large undivided testis is on the dorsal side of the gut loop. The vas deferens coils around it 6 times.

Larvae are in colonies from Heron I. collected in June and from the Philippines in January (Kott, 1980). The larval trunk, 0.6mm long, is completely enveloped in *Prochloron* cells, leaving naked patches of larval test over the sensory vesicle and in front of the adhesive organs.

REMARKS. The colonies are distinctive with their soft test, embedded *Prochloron*, and soft, mustard colour. *T. miniatum*, *T. nubilum*, *T. strigosum*, *T. paraclinides*, and *T. dispersum* (>*T. tegulum* Kott, 1984) also have embedded prochlorophytes or cyanophytes. The last two species also have the distinctive trumpet-shaped or frilly atrial siphons. *T. paraclinides* forms irregular sheets and has 8 or 9 coils of the vas deferens, but otherwise has a zooid that resembles *T. clinides*. *T. dispersum* also has similar but larger zooids. It has spicules with shorter and more separated rays, a longer larval trunk (1.0mm), dark pigment in the upper, elevated, surface of the colony, a more conspicuous bladder cell layer and the spicule size range is greater (some being nearly 0.07mm in diameter). *T. nubilum* has similar spicules, but has either a sessile atrial aperture or one produced into only a short siphon, 8 coils of the vas deferens and a very tough test. *T. strigosum*, known only from the Philippines, has very much larger spicules (to 0.08mm diameter), with fewer rays, crowded in the colonies, and it lacks an atrial siphon. *T. miniatum* differs in its globular spicules and sessile atrial apertures.

Trididemnum cristatum sp. nov.
(Figs 123C–E, 175H)

Didemnum mortenseni: Kott, 1954: 163 (part, specimen AM Y2321 from BANZARE statn 115).
Not *Didemnum mortenseni*: Kott, 1954: 163 (part, specimens from BANZARE statn 115, <*Polysyncraton tasmanense*; statn 113).

TYPE LOCALITY. Tasmania (north-eastern coast, BANZARE statn 115 676-128m, March 1931, holotype AM Y2321).

FURTHER RECORDS. Victoria (Phillip I., MV F70208).

COLONY. Colonies form extensive thin sheets, white or cream in preservative. They are hard, brittle, and encrust calcareous debris. A superficial bladder cell layer has spicules projecting into it over the anterior end of each zooid, giving the appearance of small rounded papillae. Elsewhere spicules are evenly spaced and crowded in the holotype but not particularly crowded in the other specimen. Clumps of spicules are crowded in the siphons obscuring the branchial apertures.

Spicules are large and stellate, to 0.09mm in diameter, with 9–11 long conical or flattened rays in optical transverse section. Ray length/ spicule diameter ratio is 0.35. Tips of the rays are pointed, chisel-shaped, or partially divided into 2, or with 2 points at the tip, or comb-like with 3 points along the free edge.

The common cloacal cavity is a large horizontal space at thorax level and common cloacal apertures with plain rims are randomly placed over the surface of the colony. Zooids are in clumps surrounded by deep primary canals, but these do not extend posterior to the zooids.

ZOOIDS. Zooids are small and brown, but few aspects of the structure could be determined in the small fragments of the holotype colony. Both apertures are on small siphons, each surrounded by a sphincter muscle. The branchial sac is contracted but about 8 stigmata in the anterior row and an appreciable unperforated area anterior to it were detected. A small endostylar pigment cap is present. A short, stout retractor muscle projects from the posterior end of the thorax. A few embryos are developing in the basal test. Larvae have a trunk 0.55mm long with the tail wound three quarters of the way around, and 4 long club-shaped lateral ampullae along each side of the antero-median adhesive organs, a short external ampulla on the left side of the trunk near the base of the endostyle and 3 rows of stigmata in the larval pharynx. A distinct waist separates the adhesive array from the larval oozooid and a spherical yolk mass is in front of the developing gut.

REMARKS. Although the 3 rows of stigmata cannot be clearly demonstrated in the adult pharynx, the present species is assigned to *Trididemnum* on the basis of the atrial siphon, small zooids, endostylar pigment cap, retractor muscle, a

long prestigmatal area in the pharynx and certain features of the larva. Although both *Didemnum* and *Trididemnum* have 3 rows of stigmata in the larval oozooid, the larvae of the present species are more like those of *Trididemnum*, having long club-shaped lateral ampullae, distinct waist around the trunk separating the ampullae from the oozooid, and a spherical yolk mass — all features of *Trididemnum* larvae.

The holotype of the present species (AM Y2321) and a specimen (AM Y1542) of another *Trididemnum* species with larger spicules (to 0.109mm diameter) with more rays (11–13) are 2 of the 3 specimens which Kott (1954) assigned to *Polysyncraton mortenseni*. The third specimen (AM Y1541) is *Polysyncraton tasmanense* although the gonads with 5 male follicles and 3 or 4 coils of the vas deferens are no longer evident. Spicules of *T. cristatum*, while a similar size to those of some other *Trididemnum* spp. include those with chisel-, comb-shaped and divided rays which distinguish them from other known didemnid species.

Trididemnum crystallinum sp. nov. (Figs 124, 173G)

TYPE LOCALITY. Northern Territory (Gulf of Carpentaria, Station 68 Southern Surveyor, dredge 21m, coll. S. Cook, J. Johnson 31.11.91, holotype QM G302608).

COLONY. The colony is a 5cm long fragment of a complex 3-dimensional gelatinous mass with a thick spicule-free superficial layer of bladder cells. Streaks and patches of crowded spicules are in the surface test beneath the bladder cells. Spicules are absent elsewhere. Clumps of zooids open to the surface amongst the spicules and 3 small triangular clumps of spicules are in each branchial aperture. Dark black pigment is in irregular patches in the gelatinous areas between the spicule patches and in the rims of the large sessile common cloacal apertures which perforate the surface of the colony. Some deep pits and perforations in the surface result from folding and fusing of the colony so that some external surfaces with zooid openings from them are enclosed. Also in the surface of the colony are some irregular swellings and ridges. Common cloacal cavities are large posterior abdominal spaces. Large crustacean commensals are in the common cloacal cavities.

Spicules are relatively small, occasionally to 0.05mm diameter, but usually less. Some have numerous long club-shaped rays, but others are stellate with 9–11 conical rays in optical transverse section. They appear to break up readily.

ZOOIDS. Zooids are moderately large (the thorax about 1mm long). Branchial lobes are well defined and pointed. A small atrial aperture is on a short posteriorly directed siphon from the posterior end of the dorsal surface of the thorax. About 10 fine longitudinal thoracic muscles are conspicuous in the parietal body wall anteriorly. The retractor muscle, from the upper to middle part of the oesophagus varies in length and thickness with contraction.

About 12 stigmata are in the anterior row reducing to 9 posteriorly and extensive unperforated bands of pharyngeal wall are anterior and posterior to the perforated area. The gut loop is simple and vertical with an egg-shaped stomach, a relatively long duodenum and an oval posterior stomach in the pole of the loop. Neither larvae nor gonads were detected.

Neither dark squamous epithelium nor an endostylar cap was detected on these zooids.

REMARKS. The holotype colony shares its almost aspicular condition, relatively small spicules and complex colony with *T. nobile* from which it is distinguished by the presence of some spicules with relatively numerous rod- or club-shaped rays, while *T. nobile* has only spicules with conical rays. Other species with spicules in a single layer and a thick spicule-free superficial bladder cell layer (e.g. *T. savignii, T. areolatum, T. natalense, T. discrepans*) have endostylar pigment caps and black squamous epithelium and do not have complex colonies. Although the black pigment may have been lost in preservative, the present species can be readily distinguished by its small spicules, some with numerous long cylindrical to club-shaped rays. The oval groups of zooids in *T. nube* Monniot, 1991 (from New Caledonia) may be like the present species, and the patches of spicules separated by gelatinous test are also like *T. nube* although in the latter species the spicules form a sort of capsule around the group of zooids at oesophageal level. Also, the spicules are quite different, those of *T. nube* being 0.08mm in diameter. *T. spongia* Monniot, 1991 has larger spicules and they are crowded throughout. *T. sibogae* has similar complex colonies but large spicules to 0.1mm diameter or more.

Trididemnum cyclops Michaelsen, 1921 (Figs 125A-C, 174D)

Trididemnum cyclops Michaelsen, 1921: 19. Hastings, 1931: 89. Kott, 1962: 581; 1966: 286; 1977, 616 (part); 1980:

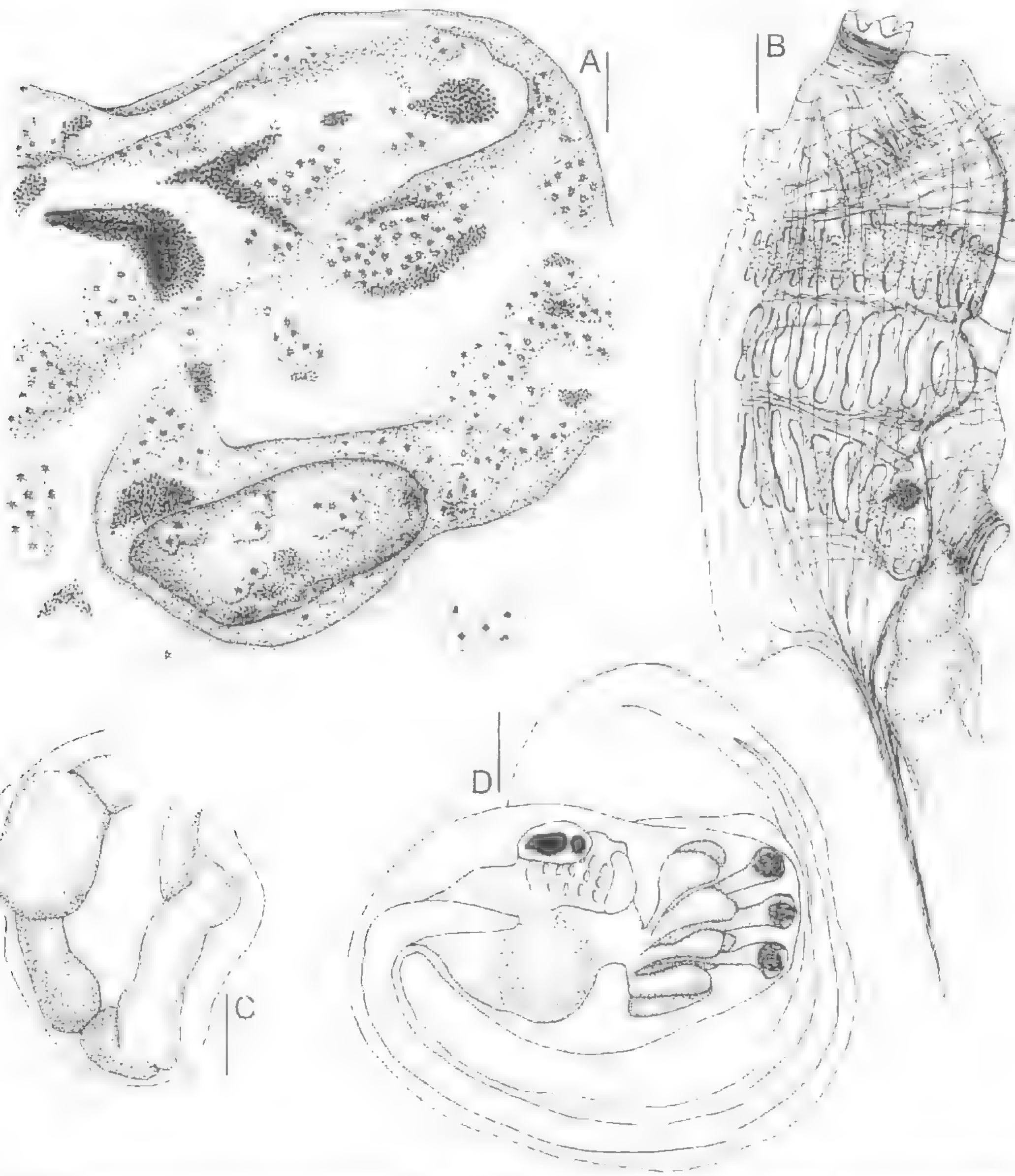


FIG. 124. *Trididemnum crystallinum* sp. nov. (QM G302608) - A, part of colony showing overgrowth on surface, a large common cloacal aperture, and some patches of pigment; B, thorax; C, ventral view of gut loop; D, larva. Scales: A, 2.0mm; B–D, 0.1mm.

10; 1981: 188; 1982a: 111; 1998: 91. Eldredge, 1967: 183. Tokioka, 1967: 85 (part). Thorne, Newcomb & Osmond, 1977: 575. Monniot & Monniot, 1987: 20 (part, fig. 2G, I; see also *T. paracyclops*); 1996: 150. Monniot, 1991: 520.

Not *Trididemnum cyclops*: Newcomb & Pugh, 1975: 534 (= *Didemnum* sp.).

Lissoclinum pulvinum: Tokioka, 1967: 97 (part).

NEW RECORDS. Queensland (Heron I., QM G9446, G9942 G301593, G301597, G301972, G302374, G308152; Magnetic I., QM G301594; Orpheus I., QM G301595).

PREVIOUSLY RECORDED. Western Australia (Ashmore Reef, WAM 255-6.87). Queensland (Heron I. – Kott, 1962, 1977, 1980; Keeper Reef, Magnetic I., Lizard I. – Kott, 1977; Low Is – Hastings, 1931). Northern Territory (Darwin – Kott, 1966). New Caledonia (Monniot, 1991). Palau Is (Kott, 1982a). Caroline Is (Kott, 1982a). Kiribati (Tokioka, 1967). Eniwetak (Eldredge, 1967). Philippines (Tokioka, 1967). Fiji (1980). French Polynesia (Monniot & Monniot, 1987). West Indian Ocean (Malagasy – Michaelsen, 1921).

Although the type location is Malagasy (Michaelsen, 1921) there have not been subsequent records from the Indian Ocean. Undoubtedly the species has been overlooked and in due course will be found in Western Australian and other tropical locations. It occupies cryptic, shaded habitats on weed, coral and rocks just below low water. It is found with other small didemnid-algal symbioses, e.g. *T. miniatum*, *Lissoclinum bistratum* and *Diplosoma virens*.

COLONY. Colonies are small, oval flat-topped cushions, usually less than 1cm long. A superficial layer of bladder cells is particularly conspicuous around the outer margin of the colony. A layer of crowded spicules is beneath the bladder cells around the outer margin, although spicules often are sparse over the upper surface, exposing the *Prochloron* symbionts (which are in the thoracic cloacal cavity) to the light. Spicules also are crowded in a layer in the basal test beneath the thoracic common cloacal cavity, but become less crowded toward the base of the colony. Zooids are arranged around the outer margin of the colony, their ventral border embedded in the marginal test, their dorsal borders exposed to the central cloacal cavity. From the surface, the endostylar pigment cap over the anterior end of the endostyle, and inside that, the branchial aperture of each zooid can both be seen interrupting the spicules around the margin of the colony. Spicules generally are to 0.04mm diameter although some are larger (to 0.06mm). Some are burr-like with crowded cylindrical rays, and others have 13–15 short conical rays in optical transverse section.

Colonies subdivide when more than 0.5cm long, a constriction from the outer margin extending across the upper surface of the colony and dividing it from surface to base (Kott, 1980). *Prochloron* are the only symbiotic plant cells in this species.

ZOOIDS. Zooids are to 1.5mm long. Branchial siphons are robust, the rim of the aperture divided into 6 rounded lobes. The atrial aperture is a sessile transverse opening across the middle of the thorax. The lateral organ is near the anterior end of the second row of stigmata, about halfway across the side of the body. About 7 long, rectangular stigmata are in each of the 3 rows. A fine retractor muscle is free from the upper part of the vertical oesophageal neck, near the posterior end of the thorax. The gut loop is bent ventrally at the base of the oesophagus. The rather flat undivided testis is behind the gut loop, with 6 coils of the vas deferens around it.

Larvae are present in colonies (QM G9942) collected from Heron I. in December and colonies from Keeper Reef in August, Fiji in July and French Polynesia (Monniot & Monniot, 1987). They are small, the trunk about 0.6–0.7mm long with only 2 antero-median adhesive organs, and 2 pairs of finger-like ectodermal ampullae. The tail is wound three quarters of the way around the trunk. The larval trunk is enveloped in *Prochloron*, absent from windows over the sensory vesicle and in front of the adhesive organs.

REMARKS. The species is distinguished by its small colonies with single systems, endostylar pigment cap, 6 coils of the vas deferens, retractor from the upper half of the oesophageal neck, and the larvae with 2 adhesive organs, 2 pairs of ectodermal ampullae and the trunk completely enveloped in *Prochloron*. *T. paracyclops* is a related species with an endostylar pigment cap and 2 larval adhesive organs, but it has larger colonies with numerous systems, 9 or 10 coils of the vas deferens, the retractor muscle from the lower (distal) half of the oesophageal neck, a longer larval trunk (about 1.0mm long), 3 or 4 pairs of larval ectodermal ampullae and the *Prochloron* transferred to the next generation by a cap of *Prochloron* cells adhering around the posterior end of the larval trunk (as in *Lissoclinum).*

Monniot & Monniot (1987) assigned specimens of both *T. cyclops* and *T. paracyclops* to the former species and invoked a great degree of intra-specific variation to justify the differences observed. Certain specimens (Monniot & Monniot, 1987: 19, fig. 2C-F, H) are characteristic of *T. paracyclops*, having the same large number of vas deferens coils, the same retractor muscle from the distal end of the oesophageal neck and the same large larva with a relatively short tail. Others (Monniot & Monniot, 1987: 19, fig. 2G, I) are undoubtedly *T. cyclops*. Neither Monniot & Monniot (1987), nor Monniot (1991) recorded the position of the plant cells on the larval trunk. Further although the posterior end of the trunk above the tail protrudes slightly, it is not a rastrum as they state (the rastrum being a T-shaped outgrowth of the larval haemocoel and trunk wall in certain *Diplosoma* spp.). The small dorsal branchial lobe reported to be characteristic of *T. cyclops* (Monniot & Monniot, 1987) was not observed in the Australian material.

T. cyclops: Monniot & Monniot, 1987 is said to be distinguished by the position of its lateral

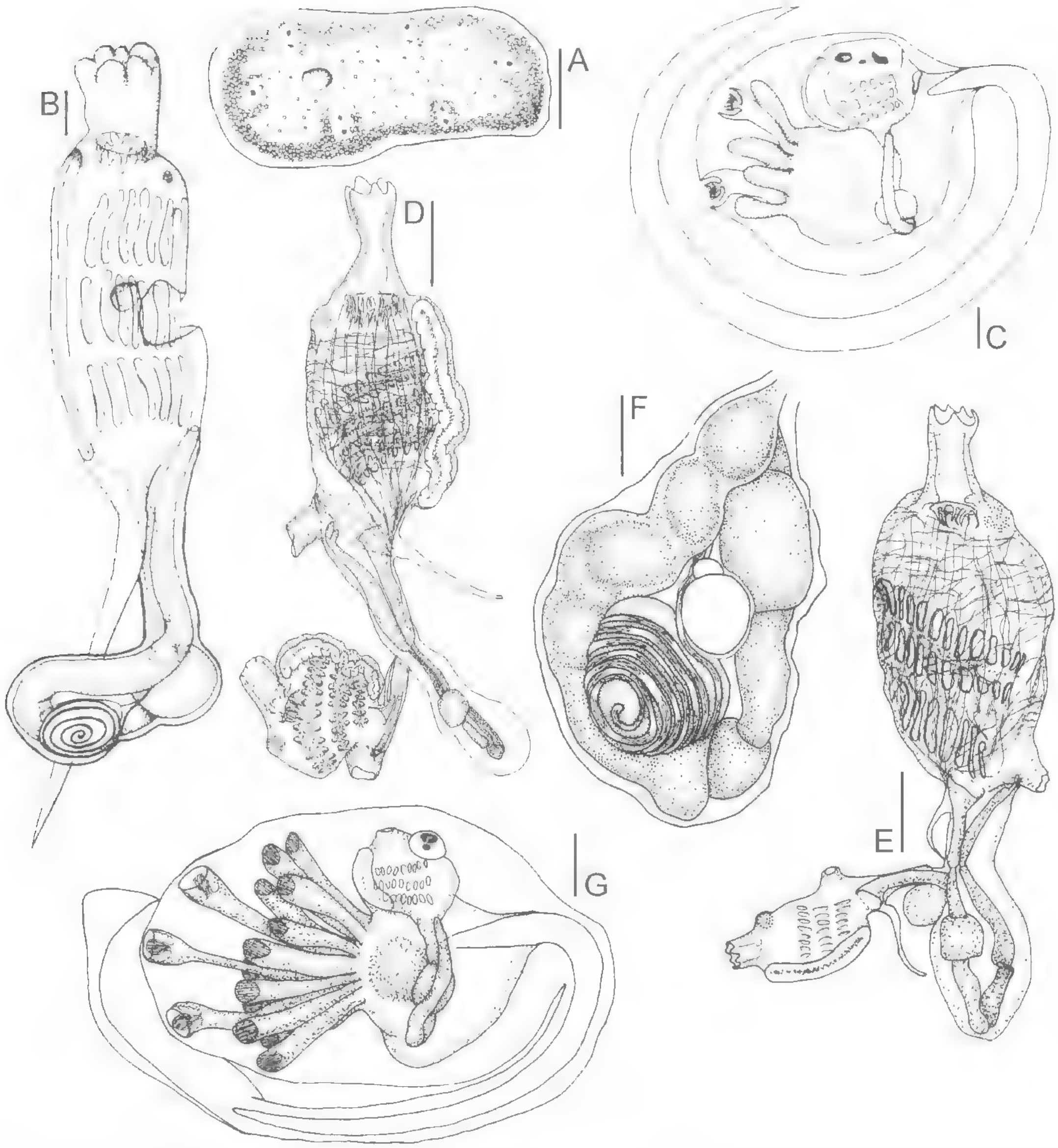


FIG. 125. A–C, *Trididemnum cyclops* (after Kott, 1980. QM G9942) – A, colony from above, B, zooid showing endostylar pigment cap; C, larva. D–G, *Trididemnum discrepans* (D,E, WAM 199.87; F, QM G302294; G, QM G302224) – D,E, zooids vegetative phase; F, abdomen, sexual phase; G, larva. Scales. A, 0.5mm; B,C, 0.1mm; D–G, 0.2mm.

organ near the dorsal end of the third row of stigmata. This has not been confirmed in any Australian material where the lateral organ is in its usual position — near the middle of the body opposite the anterior end of the second row of stigmata, its position affected by contraction of the atrial aperture.

Kott (1982a) included *T. symbioticum* Pérès, 1962 from the Red Sea in the synonymy of *T. cyclops* — both having etellate spicules with conical to round-tipped rays, an endostylar pigment cap. However, *T. symbioticum*, with posteriorly oriented atrial siphons, spicules crowded in the test with green plant cells, reddish pigment and embedded symbionts, is more like *T. clinides*, (which lacks the endostyle pigment cap).

Trididemnum discrepans (Sluiter, 1909) (Fig. 125D–G; Pl. 16B)

Leptoclinum discrepans Sluiter, 1909: 77.
Trididemnum discrepans: Kott, 1981: 187; 1998: 91; Monniot, 1991: 520.
Didemnopsis jolense Van Name, 1918: 147.
Trididemnum savignii var. *jolense*: Tokioka, 1967: 82 (part, not specimen from Florida).

NEW RECORDS. Western Australia (Kimberley, WAM 745.91 767.91; Rowley Shoals, WAM 858.83 QM GH2131; Montebello Is, WAM 199.87). South Australia (Kingston, QM G302294). Queensland (Capricorn Group, QM G301692, G302224; Sue I., QM GH2092; Nymph I., QM G302305; Murray I., QM G302301). Indian Ocean (Cocos Keeling, WAM 608.89). Thailand (Phuket, QM G300938).

PREVIOUSLY RECORDED. Australia (Green I. – QM G12477 Kott, 1981). New Caledonia (Monniot, 1991). Fiji (Kott, 1981); Indonesia (Sluiter, 1909). Philippines (Van Name, 1918; Tokioka, 1967). Palau Is and Kiribati (Tokioka, 1967).

COLONY. Colonies are gelatinous cushions to sheets with a smooth slippery surface without folds or ridges. The test is spongy with very large bladder cells, and dark pigment bodies are compressed between the bladder cells to form fusiform to irregular branched shapes. Dark squamous epithelium is around the zooids, and lines the branchial siphon. A few large common cloacal apertures interrupt the surface of the colony. A large common cloaca is beneath each aperture, and it spreads out into a horizontal cavity at thoracic level. Usually there are no spicules. However, WAM 199.87 from the Montebello Is has 3 groups of a few minute spicules in the branchial siphon and some sparse ones in the basal test. A specimen from South Australia (QM G302294) is said to have been red in life and the zooids have black squamous epithelium over the thoracic parietal body wall. Black squamous epithelium also is on the thorax of specimens from Cocos Keeling (WAM 608.89) and the Kimberly (WAM 765.91). The latter also have black squamous epithelium over the abdomen.

ZOOIDS. Zooids are long, about 2mm or more, with a long oesophageal neck. The branchial siphon is relatively short with 6 pointed lobes around the opening. The atrial siphon is short and directed horizontally and sometimes anteriorly. A pigment cap sometimes can be seen at the anterior end of the endostyle. A fine tapering retractor muscle of variable length projects out into the test from the posterior end of the thorax. The thorax is particularly wide, with up to 14 stigmata in the anterior rows. The gut loop is open, sometimes bent at right angles to the longitudinal axis of the zooid. The undivided testis has 8 coils of the vas deferens.

Large larvae are being incubated in the basal test of specimens collected in the Capricorn Group in December, from the Kimberley and Rowley Shoals in August and from Cocos Keeling in February. The trunk is 1.4mm long, with the tail wound halfway around it. Six ectodermal ampullae are along each side of the 3 antero-median adhesive organs. The ectodermal ampullae are curved and flattened at the tip — concave on the median surface and convex on the outside surface. Each has an arc of columnar cells across the distal edge.

REMARKS. The species is distinguished by its gelatinous, fleshy black colonies, virtual absence of spicules, large zooids, with more numerous stigmata than most species of this genus, and large larvae with 6 pairs of ectodermal ampullae. *T. savignii* is related (with similar large bladder cells mixed with black pigment bodies in the surface), although it has a layer of large spicules beneath the pigmented surface layer of bladder cells and a smaller larval trunk.

Larvae from Fijian colonies (Kott, 1981) are about the same size as those from the newly recorded material. Although Kott recorded only 4 pairs of ectodermal ampullae for this species, on re-examination of the material (from Malevu) the number has been found to vary from 4–6 pairs. Monniot (1991) did not record larvae from New Caledonia, but the specimens described appear to be conspecific with the present species. The larvae of colonies from Kiribati (Tokioka, 1967) are about the same size as those from other locations although, like some of those from Fiji, they have only 4 pairs of ampullae.

The colony from Florida (Tokioka, 1967), is a convoluted colony like that of *T. sibogae* — a species not otherwise known from the Atlantic, and at this stage its identity is doubtful .

The species has a wide range, and in Australian waters it is found in both temperate and tropical waters.

Trididemnum dispersum (Sluiter, 1909) (Figs 126A,B, 174B,C)

Didemnum dispersum Sluiter, 1909: 54.
Trididemnum dispersum: Kott, 1998: 91.
Trididemnum tegulum Kott, 1984: 515. Cox et al., 1985: 151.
Trididemnum sp. ('tegulum'): Parry, 1984a: 503.

NEW RECORDS. Western Australia (Shark Bay, WAM 1054.83). Queensland (Heron I., G301736, G301780,

G308012, G308315). Northern Territory (Torres Strait, South Ledge Reef, QM G300963).

PREVIOUSLY RECORDED. Queensland (Capricorn Group – Kott, 1984). Indonesia (syntypes ZMA TU443.1, TU443.2 Sluiter, 1909).

The species occupies the same cryptic habitats as other didemnid-algal symbioses — on weed and coral boulders near low tide, near the edge of the coral reefs. It is inconspicuous and the new record from Western Australia suggests that it may have a wide Indo-West Pacific range.

COLONY. Colonies are firm (but not tough), dark brown-black, hemispherical or wedge-shaped with a raised, highly arched upper surface, to 1cm in greatest dimension and to 6mm thick. They are widest near the top of the colony and narrow toward the base. Colonies probably lobulate, maintaining their small size and (usually) single cloacal system, with a large, almost sessile common cloacal aperture in the centre of the upper surface. The common cloacal cavity extends from the upper surface around the sides of the colony at abdominal level. It surrounds a central core of test that projects up from the base of the colony and sometimes forms a plug in the cloacal aperture.

Clumps of spicules are in the test around the branchial apertures but these are the only spicules that invade the superficial layer of bladder cells that surrounds the colony. Spicules are moderately crowded to sparse in a thin layer beneath the bladder cells around the upper part of the colony, but are sparse, or absent altogether at thoracic level. Beneath the abdominal cloacal cavity, they are evenly spaced but never crowded and they do not form a layer beneath the superficial bladder cells around this lower half of the colony. A small group of spicules is clustered around the opening of each atrial aperture into the common cloacal cavity. Spicules are to 0.068mm in diameter, some stellate with from 7–9 short conical rays in optical transverse section, and others burr-like or globular, with crowded rod-like cylindrical, sometimes pointed or flat-tipped but sometimes round-tipped rays (like slate-pencil-urchin spines). The conical rays of the stellate spicules often break up into needle-like spines. Ray length/spicule diameter ratio of the stellate spicules is about 0.2.

Algal symbionts, the cyanophyte *Synechocystis trididemni* (Cyanophyta) (see Cox et al., 1985), are in the bladder cell layer and the upper layers of test to thoracic level, although they tend to become progressively less crowded away from the upper surface. They are not either in or beneath the common cloacal cavity. Minute (0.005mm) diameter dark pigment cells are also in the upper half of the colony (beneath the bladder cell layer), around the common cloaca and in large lacunae in the basal test of preserved specimens. This dark pigment causes the opaque brown-black colour in the upper half of the colony, which gradually changes to the off-white colour of the lower half where the colour results from the embedded spicules and absence of black pigment. Except for those in the bladder cell layer, the dark pigment masks the symbionts in the upper half of the colony. In preservative, the colour of the symbionts fades more rapidly than the black, or dark purple pigment cells which remain dark for a time. These also fade to white after 10 years. Small spherical or rod-shaped pink cells 0.007 –0.009mm in diameter are present among the green symbionts.

Terminal ampullae of the long, branched vascular stolons are evident around the base of the colony.

ZOOIDS. Zooids are 1mm or more long. The branchial siphon is large with conspicuously pointed lobes. The atrial siphon also is large, flared and directed posteriorly. A long un-perforated pre-branchial area and 3 rows of 9 long, oval stigmata are in the pharynx. A tapering retractor of varying length projects from the middle of the long oesophageal neck. The undivided testis is against the dorsal (under) side of the gut loop, which is bent ventrally at right angles to the long axis of the zooid. The vas deferens coils 5 times around the turnip-shaped testis.

Larvae, in colonies collected in June but not in those collected in January or August, are large, the trunk being 1.0mm long. Cyanophyte cells embedded in the larval test obscure its structure, as usual being absent only from an area in front of the adhesive organs, and above the sensory vesicle. When the cells are removed there are seen to be 3 or 4 adhesive organs (the fourth resulting from subdivision of the dorsal one) and 2 ectodermal ampullae on each side.

REMARKS. Re-examination of the syntypes (ZMA TU443.1, TU443.2) of *T. dispersum* (Sluiter, 1909) show it to be the senior synonym of *T. tegulum*. The syntypes are small colonies 5–15mm long and about 2mm thick, yellowish brown in alcohol. The test is tough, with a conspicuous superficial layer of bladder cells over a crowded layer of spicules. Spicules are sparse at thoracic and abdominal level and become sparser toward the base of the colony.

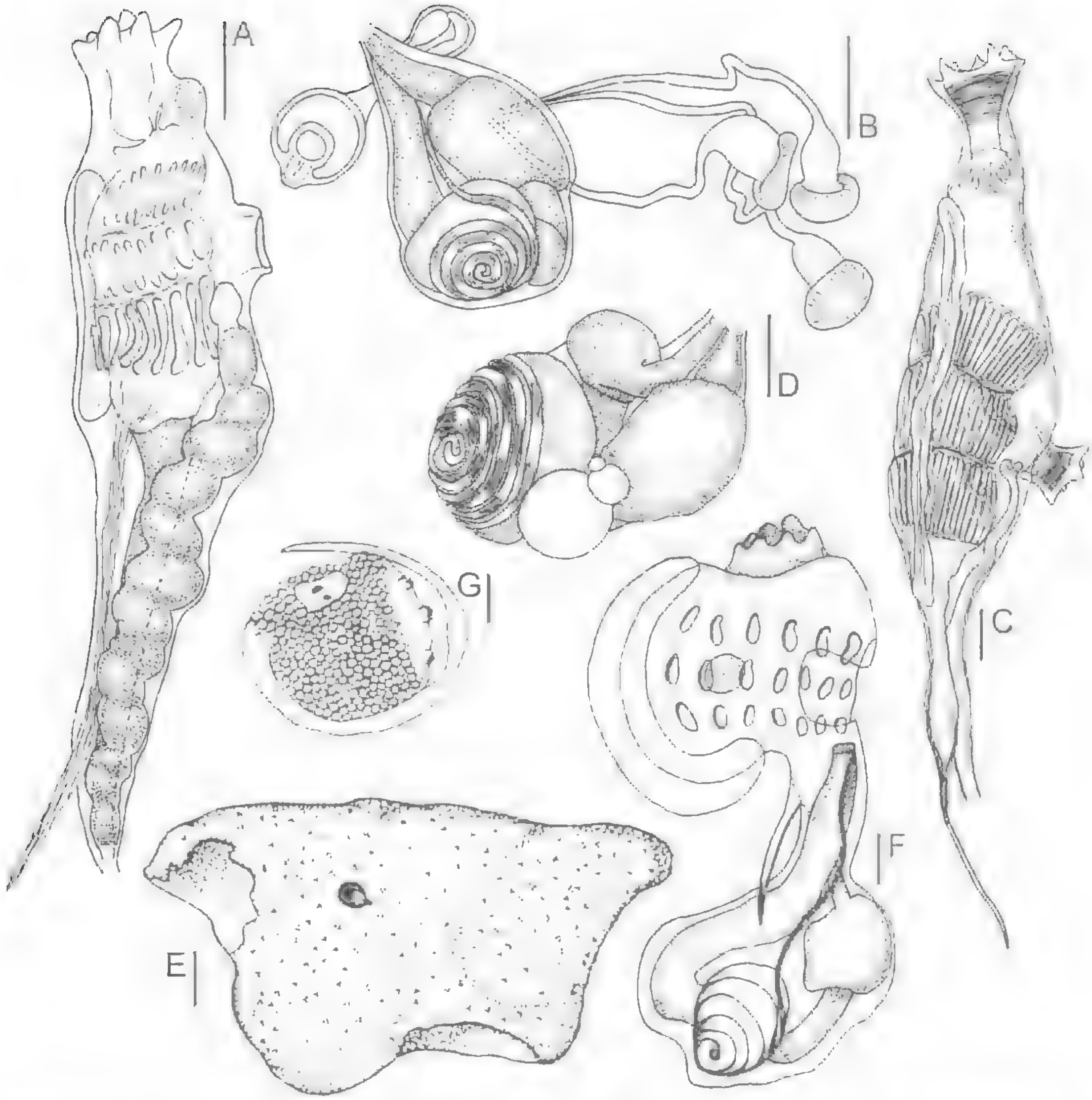


FIG. 126. A, B, *Tridideminum dispersum* (QM G300963) – A, thorax; B, abdomen showing oesophageal buds and stolonic vessles. C, D, *Tridideminum lapidosum* sp. nov.(C, QM G304634; D, QM G306111) – C, thorax, D, abdomen. E–G, *Tridideminum miniatum* (after Kott, 1980, QM G12478) E, colony; F, zooid; G, larva covered in coat of *Prochloron* cells. Scales: A,B,F,G, 0.1mm; C,D, 0.2mm; E, 1.0mm.

Although Sluiter (1909) referred to spicules to 0.038mm in diameter, re-examination showed them to be up to 0.06mm (but generally less), most with 9–11 short conical rays in optical transverse section, widely separated from one another on the large spherical central mass. The largest spicules are burr-like with narrow rod-like rays. Plant symbionts were not detected in the long term alcohol preserved syntype colonies.

Kott (1984) compared specimens of *T. tegulum* (<*T. dispersum*) with *T. clinides*, both having similar zooids with flaring posteriorly directed atrial siphons. The present species is distinguished from *T. clinides* by its highly arched upper surface and black-brown opaque colonies. Zooids of *T. clinides* are smaller, with only 5 or 6 stigmata per row, the spicules have longer rays, *Prochloron* and the cyanophyte *Synechocystis* are embedded in the test and the larvae are smaller. *T. dispersum* contains the cyanophyte and lacks *Prochloron* (Cox et al., 1985). The

short retractor muscles Kott (1984) reported are not seen in the newly recorded colony.

Trididemnum lapidosum sp. nov.
(Figs 126C,D, 175C; Pl. 16C,D)

TYPE LOCALITY. Western Australia (NW of Surrurier I. – Long I. – 21°33.5'S 114°40.0'E, 18m, coll. AIMS Bioactivity Group 21.8.88, holotype: QM G308687; Houtman's Abrolhos 28°40'S 113°50'E, coll. C. Bryce, paratype QM G304634).

FURTHER RECORDS. Western Australia (northwest of Port Hedland, QM G306111; Houtman's Abrolhos, WAM 768.88).

The species has been taken from 18m and 28m.

COLONY. The holotype and paratype colonies form large (to 10cm high) complex, robust, probably upright paddle-shaped lamellae 0.5–1cm thick, crowded with spicules throughout. Large, slightly elevated common cloacal apertures, about 1cm apart, open on both sides of the lamellae and around the edges. Zooid openings are also on both sides, interrupted by irregular narrow white, opaque streaks of unperforated test on the surface and sometimes protruding from it. A hard middle layer of spicule-filled test separates the layer of zooids on each side. A hard flat branching core of packed spicules forms an internal skeleton in the middle layer of test (which appears to be a fusion of the basal surface folded back on itself). The external surfaces are more or less smooth and even. Another specimen (QM G306111) is a robust slab with zooids opening on both sides, and the other (WAM 768.88) is an encrusting sheet with zooid openings only on one (the upper) surface. Except in the internal plate-like skeleton, spicules are evenly distributed but not especially crowded. All surfaces are hard and raspy with large pointed spicule-rays projecting from them.

The branchial apertures are stellate, their margins lined with a single row of the large spicules. Sometimes the lobes of the branchial apertures project from the surface like little warts. The atrial openings into the oesophageal common cloacal cavity are marked by 5 small groups of spicules.

Internally, colonies are like stiff pieces of honeycomb, the hard spicule-filled test interrupted by oesophageal cloacal cavities, the rigid compartments in which the thoraces are contained and sponge-like spaces (some in the lower half of the colony containing debris). The long oesophageal necks of the zooids with their retractor muscles join the thoraces to abdomina (embedded in the central or basal test) through the firm connectives that traverse the large oesophageal cloacal cavities. Spicules are large, up to 0.16mm diameter with 9–11 moderately pointed rays in optical transverse section. Ray length/spicule diameter ratio is about 0.35.

In life the holotype colony was white to beige externally with orange-yellow zooids. In preserved colonies brownish coloured spherical cells are in the upper layer of test around the thoraces (see WAM 768.88, QM G304634, G306111), although they were not detected in the holotype.

ZOOIDS. Zooids are large, about 3mm long, the thorax, oesophageal neck and abdomen each comprising about one-third of the total length. The branchial siphon is relatively short with 6 narrow, pointed lobes around the apertures and a distinct sphincter muscle around the siphon. A short posteriorly or laterally oriented atrial siphon from between the second and third rows of stigmata also has a conspicuous sphincter muscle and the rim of the aperture has 5 pointed lobes. Circular lateral organs are each side of the postero-dorsal part of the thorax about level with the third row of stigmata. A robust retractor muscle from about halfway down the oesophageal neck tapers to a long, slender point. Almost the anterior third of the pharynx is imperforate. The stigmata are long and narrow and 16 are in the anterior row, 15 in the middle row and about 12 in the posterior row. The oesophageal neck is long. The rounded stomach is in the distal almost spherical part of the abdomen and the post pyloric section of the gut is relatively short and curved up over the undivided testis which is against the dorsal part of the pole of the gut loop. The vas deferens has 7 coils. Larvae are not known.

REMARKS. Spicules are similar in size and form to those of *T. sibogae*, but colonies of *T. lapidosum* lack a posterior abdominal component of the common cloacal cavity and are never as complex as *T. sibogae*, zooids are larger with more stigmata per row, a long oesphageal neck and the retractor muscle projecting from halfway down (rather than from the top of the oesophagus as in *T. sibogae*). The colony lobes are flat lamellae rather than the cylindrical lobes of *T. amiculum*. Unlike the latter species (in which it is almost one-third of the zooid length), the branchial siphon is only a fraction of the length of the thorax and spicules are evenly distributed throughout. An endostylar pigment cap and black

squamous ectoderm of the *savignii* group of this genus were not detected.

Like many other *Trididemnum* species the atrial siphon, with 5 points around the rim of the opening, is reminiscent of *Leptoclinides*.

Trididemnum miniatum Kott, 1977
(Figs 126E–G, 173D,E)

Trididemnum miniatum Kott, 1977: 617; 1980: 7; 1982a: 111; 1998: 91. Parry, 1984a: 503. Parry & Kott, 1988: 151. Monniot, 1991: 522.
Trididemnum viride: Tokioka, 1967: 8 (part, colonies with smaller spicules).
Didemnum dealbatum Sluiter, 1909: 55 (part, colonies from statn 301).

NEW RECORDS. Queensland (Heron I. QM G301592, G301599, G301602-3, G301972, G302025; Lodestone Reef, QM G301596).

PREVIOUSLY RECORDED. Queensland (Capricorn Group – Syntypes QM G9927 Kott, 1977, 1980; Green I. – QM G12478 Kott, 1980; Deltaic Reef – Kott, 1982a). Philippines (part of USNM 11661, 11796 Tokioka, 1967). New Caledonia (Monniot, 1991). Indonesia (ZMA TU441.2).

The species occupies cryptic habitats in shallow water behind the reef crest and in lagoons. It is found attached to sea grass blades and *Halimeda*, on open reef flats. It is found often with equally small colonies of *Diplosoma virens* where tidal currents are strong, suggesting that small colony size is an adaptive advantage in these habitats.

COLONY. Colonies are small cushions to 1cm in maximum extent, but often only about 4mm, attached lightly to the substrate by strands of test. In life, they are white to emerald- or lime-green, depending on the distribution of spicules, and usually fine veins of red pigment are in the surface test. The concentration of spicules in the superficial layer of test, where algal cells are most crowded varies according to the amount of light striking the colony. Throughout the remainder of the test, spicules are in moderate concentrations providing a white background for the green cells that are embedded in the surface layer. The green cells become progressively less crowded toward the base of the colony and also are present in the common cloacal cavity. Spicules usually are absent from the surface test over the anterior end of zooids, although they often are present in the linings of the branchial siphons. Spicules are small (to 0.02mm in diameter) and globular, with crowded flat-tipped cylindrical rays.

The symbiotic cells are *Prochloron* and a red filamentous cyanophyte (Parry, 1984a; Parry & Kott, 1988).

ZOOIDS. Zooids are small, to about 0.8mm long. They are orange in life but colourless in preservative. Branchial lobes are pointed. The atrial aperture is a sessile, transverse opening. A round lateral organ is in the centre of each side of the thorax. Seven stigmata are in each of the 3 rows in the branchial sac. A retractor muscle projects from the anterior part of the relatively short oesophageal neck. The gut loop is slightly flexed ventrally, and the small undivided testis against the dorsal side of the loop has 6 coils of the vas deferens around it.

Larvae are present in most of the known colonies — collected in January, May, August, October, November and December. Kott (1980) suggested that the species may breed throughout the year. The larval trunk is 0.07mm long. Three adhesive organs are in the anterior midline and 3 ectodermal ampullae are on each side of the anterior end of the trunk. *Prochloron* is embedded in the larval test, being absent only from windows in front of the adhesive apparatus, and over the sensory vesicle.

REMARKS. The small, bright green colonies with embedded *Prochloron* are distinctive. Sometimes they can be confused with colonies of *T. clinides*, although the latter species has spicules clustered together over the anterior ends of the zooids, the colonies are never such a bright green colour, and they lack the red filamentous cyanophyte that characterises *T. miniatum*. The small globular spicules are unique amongst plant-bearing *Trididemnum* spp. (which usually have stellate spicules). The zooids, with their sessile transverse opening (like that of *T. cyclops*) also distinguish the species from *T. clinides*. *T. cyclops* is distinguished by its endostylar pigment cap, and absence of embedded *Prochloron*. *T. nubilum* also has a similar zooid and embedded symbionts, but its spicules are larger and stellate rather than globular.

Monniot (1991: 523, fig. 3D) referred to 3 or 4 coils of the vas deferens, although her figure shows 6 coils, as in the Australian material. The layer of *Prochloron* embedded in the larval test is not recorded for the New Caledonian material, although other aspects of the larva are characteristic.

The specimens from Indonesia (ZMA TU441.2) assigned to *Didemnum dealbatum* Sluiter, 1909 and designated syntypes (with ZMA TU441.1) by Spoel (1969) were, on re-examination, found to be the present species. The colonies are small, soft, fleshy, irregular

cushions with rounded margins. They break up readily. The branchial apertures form dimples in the upper surface, symbionts are embedded in the test and the usual small globular spicules are embedded throughout. Zooids are minute and the branchial sac has the usual 7 stigmata per row. Re-examination of the 2 specimens in ZMA TU441.1 has shown them to be the syntypes of *D. dealbatum*.

Trididemnum nobile sp. nov.
(Figs 127, 174F; Pl.16E,F)

Trididemnum cerebriforme: Kott, 1972b: 178 (part, specimens from Investigator Strait); 1975: 10.

Not *Trididemnum cerebriforme*: Kott, 1962: 170 (<*T. pigmentatum, T. sibogae, T. vermiforme*); 1972b: 178 (part specimens from Elliston Bay <*D. lissoclinum*); 1972c: 247 (< *T. sibogae*); 1972d: 47 (<*T. sibogae*); 1976: 64 (? *T. sibogae*). Monniot, 1991: 518 (<*T. pigmentatum*).

Leptoclinides rufus: Kott, 1972a: 16 (part, specimens from West I.).

TYPE LOCALITY. South Australia (W of Ceduna, Tourville Bay, Davenport Creek 6-8m, coll. K. Gowlett-Holmes, W. Zeidler, B.J. McHenry 5.3.93, holotype SAM E2630, paratype SAM E2633; Coobowie Bay, *Posidonia* bed, 3m silty. limpet feeding on it, coll. S.A. Shepherd August 1982, paratype QM GH2371).

NEW RECORDS. Western Australia (Port Hedland, WAM 864.83; Cervantes, WAM 394.87). South Australia (Port Bonython jetty, QM GH4233, GH4240-1, SAM E2679, E2692; West I., SAM E2444; Pearson I., SAM E2682; Willunga Reef, SAM E2541, E2685). Queensland (Caloundra, QM G308465)

PREVIOUSLY RECORDED. South Australia (Sir Joseph Banks Is – Kott, 1972b; St Vincent Gulf – Kott, 1975).

The species is said to be common in South Australia on jetty piles and on the undersurfaces of rocky overhangs. It should be noted that although records on the eastern coast do not extend north of Moreton Bay, on the western coast they extend north to Port Hedland.

COLONY. The colonies are spongy, gelatinous and translucent, growing around weed etc. They have irregular surface ridges and lobes surrounding deep depressions and sometimes the colony overgrows the surface enclosing external surfaces in internal spaces. These enclosed spaces, together with the vast posterior abdominal cloacal spaces, create the spongy consistency of the colonies. Common cloacal apertures are along the surface ridges or are terminal openings on lobes that project from the surface (WAM 394.87). The cloacal cavities are deep, surrounding clumps of zooids and extending into large posterior abdominal spaces. The terminal ampullae of stolonic vessels are conspicuous in the test. Embryos are incubated in the test beneath the posterior abdominal cloacal spaces — i.e. the homologue of basal test. Sometimes rubble and weed is incorporated in the test. Branchial apertures are on the upper surface as well as on the sides, roof and base of some of the internal spaces caused by infolding, overgrowth and fusion of the colony.

Spicules usually are most crowded, often in a single layer, beneath a thin, turgid, superficial bladder cell layer into which they project around the branchial apertures, and they are in a layer lining the common cloacal cavities. In some colonies (QM GH2371, GH4233, SAM E2679, E2685) they are patchy or sparse at thorax level. others (SAM E2630, E2633, E2685, E2692, WAM 864.83) are aspicular. Spicules are relatively small (to 0.07mm diameter), stellate, with 7–9 rather blunt, relatively short, conical rays in optical transverse section. Ray length/spicule diameter ratio is about 0.3.

In life most colonies are grey. Most also are grey in preservative owing to the black squamous epithelium on the zooids.

ZOOIDS. Zooids are about 1.5mm long, although the thorax is very contractile and variations in its size and shape are great. About 15 fine longitudinal parietal muscles extend the length of the thorax to join a short, almost rudimentary retractor muscle projecting out from the posterior end of the thorax or the top of the oesophageal neck. However, the length of the retractor undoubtedly varies with contraction becoming long and slender in some colonies (e.g. WAM 864.83). Fine transverse thoracic muscles are present in the parietal body wall around the anterior part of the thorax.

In fresh and sometimes in preserved material, the squamous epithelium of the whole or part of the abdominal and thoracic body wall, especially on the branchial siphon and around the anterior part of the thorax, is black. The shape of the cells often is affected by contraction or distortion of the body wall, but the cells always have a pale spherical nucleus in the centre. An endostylar pigment cap usually is present, although this is often faint in long-preserved material and sometimes it is obscured by the black epithelium of the thoracic wall (which is interrupted by the large circular, flat, shallow lateral organ on each side).

The atrial aperture is on a short, posteriorly oriented siphon. Eight stigmata are in the anterior row in the branchial sac, reducing to 6 in the posterior row. The distal part of the gut loop is flexed ventrally to create a double loop, with the gonads beneath this flexed part of the loop except

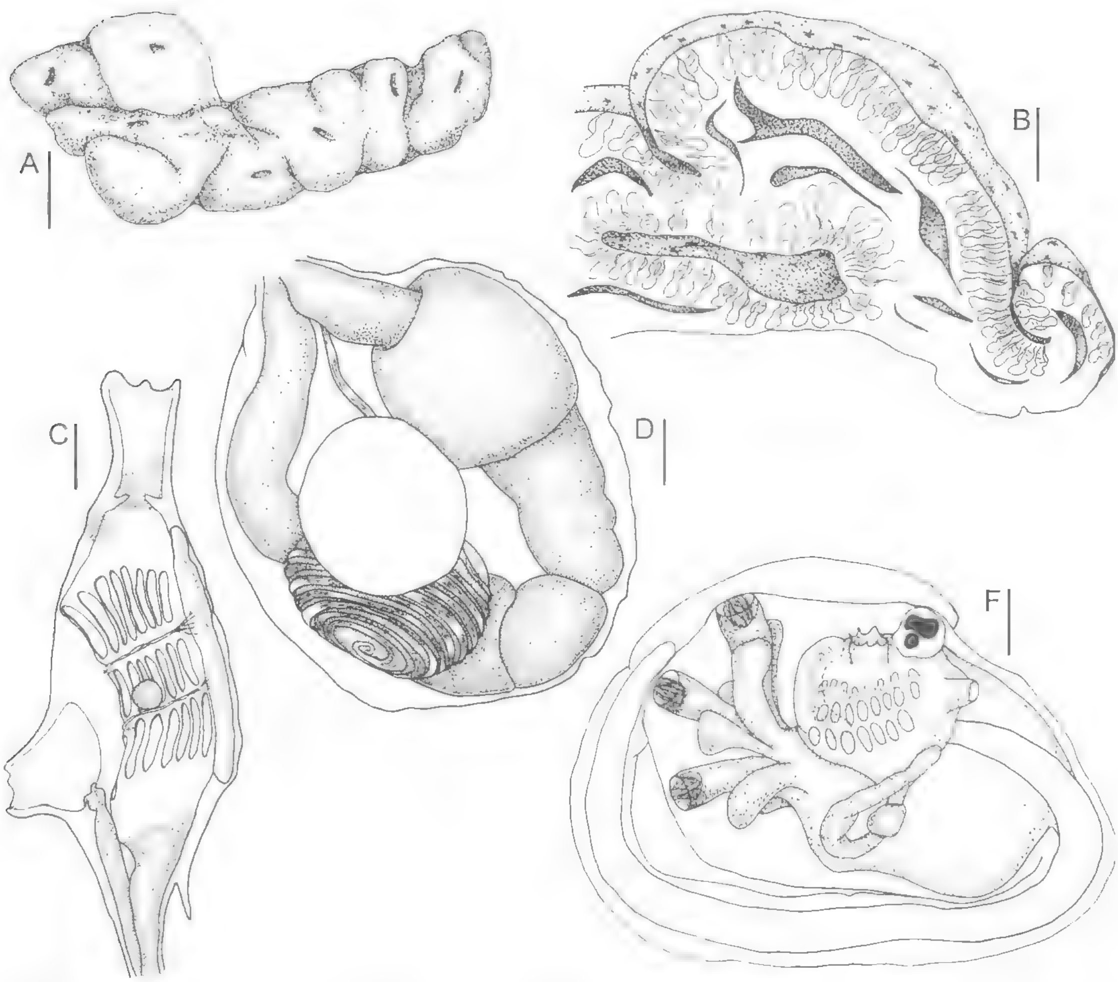


FIG. 127. *Trididemnum nobile* sp. nov. (A, QM GH4233; B, WAM 864.83; C, SAM E2444; D, SAM E2682; E, WAM 394.87) – A, colony; B, semidiagrammatic vertical section through colony showing enclosed surfaces and common cloacal cavities; C, thorax; D, abdomen; E, larva. Scales: A, 1.0cm; B, 2.0mm; C–E, 0.1mm.

in large fleshy colonies (e.g. WAM 864.83) in which zooids have long oesophageal necks, long retractor muscles and vertical gut loops. Ten coils of the vas deferens surround the large hemispherical to conical testis.

Larvae are being incubated in the basal test of spcimens collected in May (WAM 394.87), July (QM GH4233), August (QM GH2371) and November (SAM E2444). Three slender club-shaped ectodermal ampullae are along each side of the 3 antero-median adhesive organs. The distal tips of the ampullae are broad, rather flattened and curved around so that mesial surfaces are concave and outer surfaces convex. A conspicuous external horizontal ampulla projects back from the vicinity of the waist on the left side of the trunk. The larval trunk is 0.65–0.7mm long and the tail is wound halfway around it.

REMARKS. Variations in colony form appear to be related to growth, the colonies being flat sheets (QM G308465) initially but subsequently raised lobes become protuberant and overgrow the surface and one another, before fusing with some other parts of the surface. The concentrations of spicules in the colony also vary from even, albeit thin, layers beneath the surface and around the common cloacal cavities to being relatively sparse or absent altogether. Variations in the zooids result from contraction, and variations in the intensity of the black squamous epithelium on the body wall. Characters that determine the

species are the tendency to grow into a complex, convoluted colony, shape and size of the spicules (most being between 0.05 and 0.07mm diameter, with 7–9 pointed conical rays in optical transverse section), their restricted distribution (often being absent altogether), a large larval trunk with 3 pairs of lateral ampullae, and a relatively short larval tail.

T. cerebriforme Hartmeyer, 1913 from South Africa and *T. cerebriforme*: Michaelsen, 1924 from New Zealand are related to the present species. Larvae from the type locality of the nominal species (see Millar, 1955) are smaller (trunk 0.52mm long) with 4 pairs of lateral ampullae, suggesting some isolation from the present species. The New Zealand species has a particularly thick bladder cell layer.

Although its range overlaps the present species, the tropical *T. sibogae* has larger and usually more crowded spicules with longer rays and larvae with 4 ectodermal ampullae. *T. vermiforme* is another related species from southern Australia which has a similar larva. It is distinguished from present species by its spicule-free bladder cell layer, and large (to 0.09mm diameter) spicules with shorter conical rays present throughout the colony.

Other species of *Trididemnum* develop similar variable and complex sponge-like colonies with vast posterior abdominal cavities (see *savignii* group above). However, either they have more numerous spicule rays (*T. caelatum*, *T. crystallinum* and *T. pigmentatum*), or larger spicules (*T. sibogae*, *T. vermiforme*) and/or the spicules crowded throughout (*T. vermiforme*, *T. sibogae* and *T. spongia*), or the larvae have more numerous ectodermal ampullae (*T. amiculum*, *T. cerebriforme*). Of the species with complex and often partly aspicular colonies only *T. crystallinum* has relatively small stellate spicules like the present species.

Trididemnum nubilum Kott, 1980
(Figs 128A,B, 174E; Pl.16G)

Trididemnum nubilum Kott, 1980: 9; 1981: 188; 1982a: 105; 1998: 92.

Trididemnum viride: Tokioka, 1967: 87 (part, specimens with spicules with numerous rays).

NEW RECORDS. Queensland (Heron I. QM G308443).

PREVIOUSLY RECORDED. Queensland (Lizard I. – QM GH150 Kott, 1981). Philippines (USNM 11641, 11680 and part of: 11640, 11659, 11661, 11672, 11681, 11796, Tokioka, 1967; Kott, 1982a). Fiji (Kott, 1981).

COLONY. Colonies are small cushions to more extensive sheets to about 1.5mm thick, investing hard substrates (e.g. QM G308443 growing around tips of *Acropora* skeletons). They are invariably firm, and in larger colonies the surface is divided by depressions over the shallow thoracic cloacal canals. Zooid openings are along each side of these canals, ventral and posterior parts of the zooid being embedded in the test, while the dorsum of each thorax is presented to the canals.

Spicules are moderately crowded throughout the test. They appear to be less crowded over the cloacal canals only because the thinner layer of test there is more translucent than between the canals where the greater depth of uninterrupted test with its contained spicules is whiter and more opaque. Spicules are mixed with minute plant cells in the surface and in the test along each side of the cloacal canals. Most are stellate with 11–13 short, conical and pointed or rounded rays in optical transverse section. They are up to 0.05mm in diameter. Green cells are up to 0.01mm diameter and are cyanophytes (Kott, 1982a). There are no spicules on the basal surface.

Collector's notes for a colony from Heron I. report it to have been green, white and purple, although the disposition of these colours is not known.

ZOOIDS. Zooids are small, to 0.6mm long. The branchial siphon has 6 small pointed lobes around the rim of the aperture. Six stigmata are in each row in the minute thorax. The retractor muscle projects into the test from the top of the rather short oesophageal neck which is about one-third of the length of the abdomen. The atrial aperture is sessile and transverse, but sometimes it is contracted into a circular opening. The undivided testis is against the dorsal side of the gut loop with 7 coils of the vas deferens around it. A V-shaped mass of dark pigment cells are in the gut loop. These may be blood cells. They are found also in lacunae in the basal test in this and other species of Didemnidae.

Embryos are being incubated in the test in colonies collected from Heron I. in November. They begin their development in the base of the colony, and move up toward the surface as they develop, the larvae being released through the surface test rather than into the narrow common cloacal canals. The larval trunk is about 0.65mm long, with the tail wound almost halfway around it. Four or 5 adhesive organs (the middle ones sometimes subdividing) are in the antero-median line with 4 epidermal ampullae on each side, and

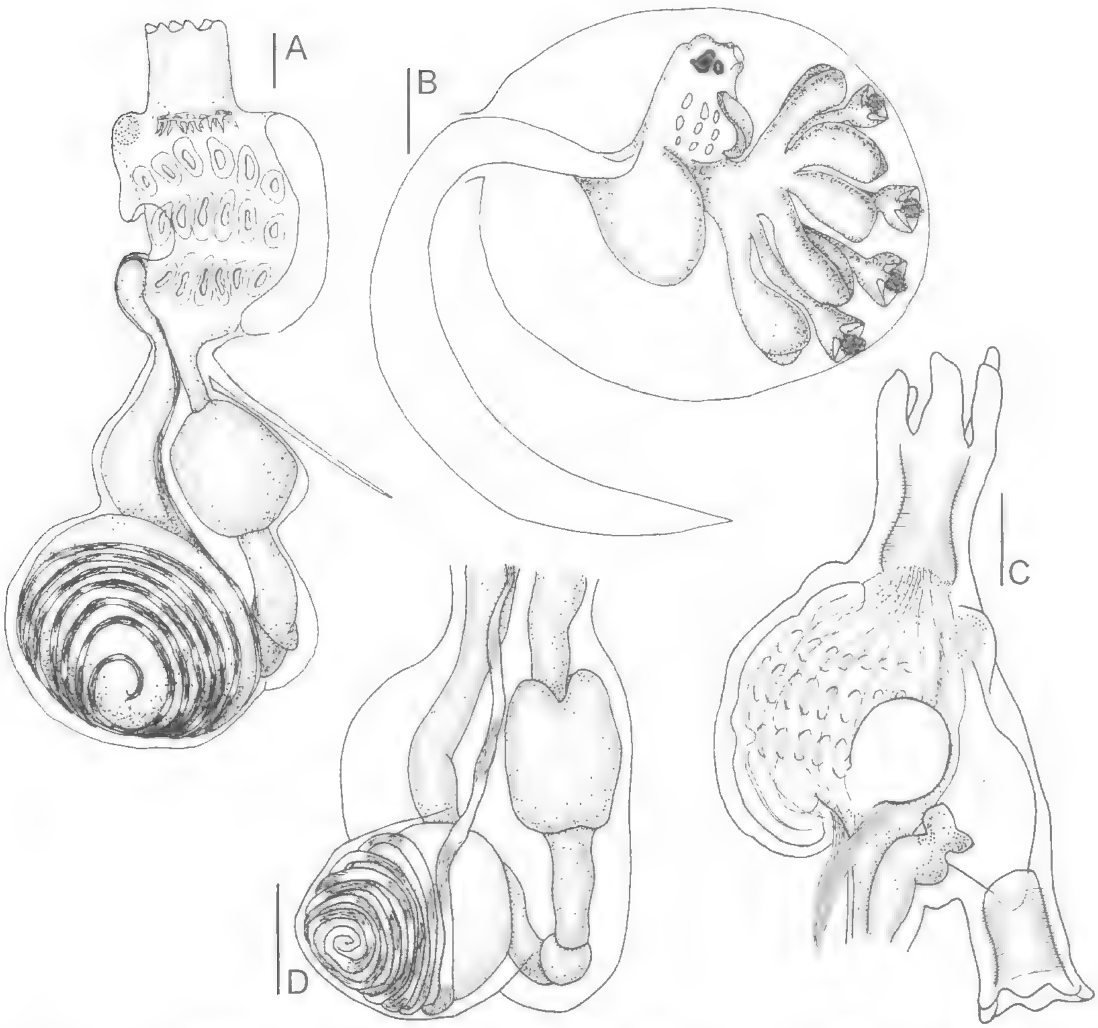


FIG. 128. A, B, *Trididemnum nubilum* (A, QM GH150; B, QM G308443) – A, zooid (after Kott, 1982a); B, larva, showing the 4 adhesive organs. C, D, *Trididemnum paraclinides* sp. nov. (WAM 617.89) – C, thorax; D, abdomen. Scales: 0.1mm.

an additional mid-dorsal one at the anterior end of the trunk. The thorax of the oozooid projects up into the larval test, and the whole oozooid is separated from the frontal adhesive organs by a narrow waist. Plant cells are embedded in the larval test, absent from a circular area over the sense organs and another in front of the adhesive organs.

REMARKS. The species is unusual, with cloacal canals rather than the larger cavities of many other species of this genus. Its zooids, with a sessile transverse atrial opening, are like *T. cyclops*, *T. paracyclops* and *T. miniatum*. Like *T. miniatum*, the plant cells are embedded rather than being in the cloacal cavity. The larvae also are distinctive, having 4 adhesive organs rather than the 2 of *T. cyclops* and *T. paracyclops*. They are like the latter species in having 4 pairs of epidermal ampullae, but the trunk is smaller. Seven coils of the vas deferens is the correct number for this species (Tokioka, 1967), despite Kott's (1980) record of 5.5 coils, and later records of Philippine specimens (Kott, 1982a) with 8.5 coils.

The larva from Basilan I. illustrated by Tokioka (1967) from a specimen (USNM 11681) assigned to *T. viride*: Tokioka, 1967 is from *T. strigosum* rather than the present species (see Kott, 1980).

The ethanol in which this species is preserved in the same pale green colour of preservative in which , *T. cyanophorum* from the Bahamas (QM GH3471) is preserved.

Trididemnum paraclinides Kott, 1982
(Figs 128C,D, 175G)

Trididemnum paraclinides Kott, 1982a: 107.
Trididemnum clinides: Kott, 1981: 186 (part, specimens from Mambualau and Dravuni).

NEW RECORDS. Indian Ocean (Cocos Keeling Is, WAM 617.89).

PREVIOUSLY RECORDED. Western Pacific (Palau Is – QM GH575 holotype Kott, 1982a; Fiji – QM GH91, GH144 paratypes Kott, 1981).

COLONY. Colonies are flat-topped cushions with rather irregular outlines and rounded margins, to 2cm in maximum dimension. A spicule-free superficial bladder cell layer gives the colonies a fleshy appearance, and beneath this are large (to 0.12mm diameter) stellate spicules moderately crowded throughout. Spicules have 11–15 conical pointed-rays in optical transverse section, although often flat stumps between the rays imply that some may have broken off. Ray length/spicule diameter ratio is about 0.25. Colours are green to a blackish-slate colour in life.

Large spherical symbiotic cells are in the test, and in the newly recorded colonies they cling to the zooids when they are removed from the colony. Branchial apertures are not evident on the surface of the preserved colonies as they are withdrawn into the soft surface layer of test. The relatively restricted common cloacal spaces are at oesophageal level.

ZOOIDS. Zooids with a contracted thorax are about 1mm long. The branchial siphon is long and conspicuous, with the border of the opening produced into 6 characteristically long lobes. The atrial siphon also is long and cylindrical and usually projects posteriorly. Cup-shaped lateral organs project laterally from each side of the posterior third of the thorax. A stumpy retractor muscle originates from the posterior end of the thorax. The gut forms an almost completely vertical loop with the usual constrictions between duodenum, posterior stomach and rectum, the latter in the pole of the loop. A large spherical testis lies against the dorsal side of the gut loop and has 7 coils of the vas deferens around it.

Larvae, present in the holotype (from the Palau Is) have 3 pairs of ectodermal ampullae and 3 antero-median adhesive organs in the anterior end of the 0.7mm long larval trunk. Plant cells are embedded in the larval test leaving only the adhesive and sense organs exposed.

REMARKS. The small thoraces with long, narrow branchial lobes are characteristic, as are the large spicules with relatively short rays. *T. areolatum* has similar spicules, and even has stumps between the rays where some appear to have broken off, but its spicule rays have blunter tips than those of the present species and its colonies are more sheet-like than the (possibly lobulated) small cushions of the present species. Further, the embedded symbionts of the present species do not occur in *T. areolatum*.

Amongst other species with small colonies, embedded symbionts, and a posteriorly oriented atrial siphon, *T. clinides* has a clump of spicules in the surface layer of test over each zooid, rather than being spicule-free, and its spicules are smaller and have fewer rays. *T. dispersum* has different and smaller spicules, some with needle-like rays.

Trididemnum paracyclops Kott, 1980
(Figs 129A–C, 174A)

Trididemnum paracyclops Kott, 1980: 12; 1981: 188; 1982a: 111; 1998: 92; Monniot, 1991: 525.
Trididemnum spiculatum Kott, 1962: 281 (part, specimen from Heron I.).
Trididemnum cyclops: Kott, 1977: 47 (part, colonies extensive sheets); Monniot & Monniot, 1987: 20 (part, larger colonies: fig. 2C-F,H).

NEW RECORDS. Queensland (Heron I., QM G301900, G302026, G302067, G302524).

PREVIOUSLY RECORDED. Queensland (Heron I.– QM G12627 holotype, G12628 paratypes Kott, 1982); Northwest I., Wilson I., Nymph I., Lizard I., – Kott, 1980). Palau Is, Guam, Philippines (Kott, 1982a). Fiji (Kott, 1981). New Caledonia (Monniot, 1991). French Polynesia (Monniot & Monniot, 1987).

The species sometimes occupies shaded habitats behind the reef crest, but is more often found in high energy locations where thin extensive sheets adhering tightly to hard substrates are difficult to dislodge. The high energy locations that the species occupies may be the reason that there are relatively few records of it. Nevertheless, it has a wide recorded range in the western Pacific. It is not yet recorded from the Indian Ocean.

COLONY. Living colonies form extensive thin green sheets, with black pigment around the irregular margins which grow around and between irregularities and protuberances in hard substrates (rather than growing over them). Branches of the colony have a tendancy to fuse with one another, and sometimes parts overgrow and fuse with the surface (Kott, 1980). Black pigment that sometimes is so conspicuous around

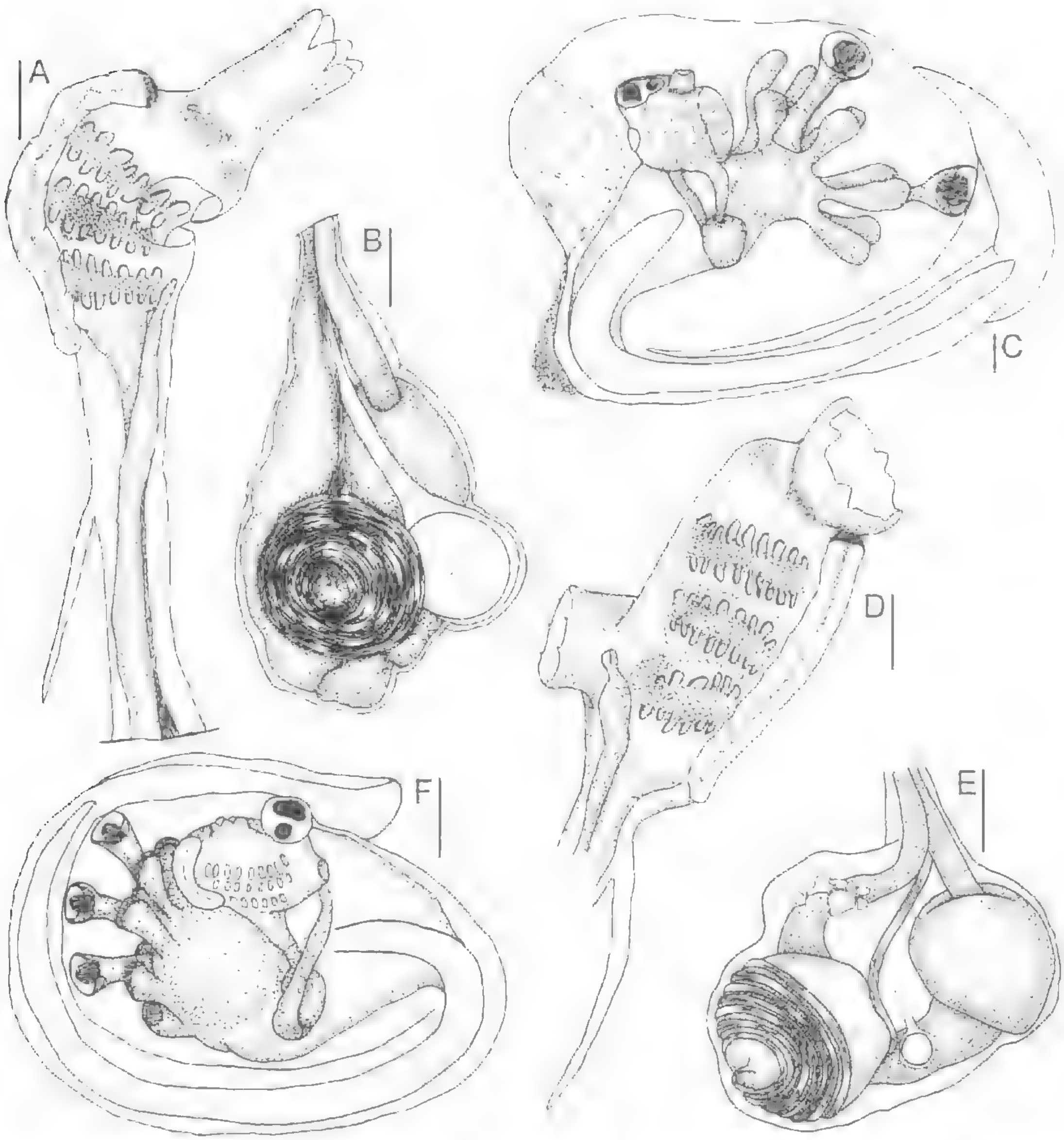


FIG. 129. A–C, *Trididemnum paracyclops* (A,B, QM G301900, C, QM G12627) – A, thorax showing endostylar pigment cap; B, abdomen; C, larva showing plant cells in concavity at posterior end of trunk. D–F. *Trididemnum pigmentatum* sp. nov. (D,F, QM G308178; F, QM G302422) – D, thorax showing endostylar pigment cap; E, abdomen; F, larva. Scales: 0.1mm.

the margins is in the basal test of preserved specimens, and dissolves into the preservative.

Spicules are in a more or less crowded layer beneath a superficial layer of bladder cells in the surface and margins of the colony although they often are less crowded in the surface, allowing light to penetrate to the *Prochloron* in the thoracic common cloacal cavity. Spicules also are crowded in a layer beneath the cloacal cavity, but become sparse in the basal half of the colony. A thin layer of spicules is on the base of the colony. They are to 0.08mm diameter, stellate, with 13–15 short, conical but not very pointed rays in optical section. Zooids are evenly distributed, and crowded. *Prochloron* are the only symbiotic cells in this species (Parry & Kott, 1988).

ZOOIDS. Zooids are up to 1.5mm long. The branchial siphon is long and robust with 6

shallow lobes around the opening. The atrial aperture is a sessile transverse opening. An endostylar pigment cap is present. The circular lateral organ is about level with the second row of stigmata. Seven long stigmata are in each of the 3 rows. The retractor muscle is thick and robust and free of the zooid from the posterior end of the long vertical oesophageal neck (the origin of the retractor muscle from the upper part of the oesophageal neck in Kott, 1980, fig.15 is incorrect). The posterior end of the gut loop is relatively short and is flexed ventrally with the undivided testis behind it. The vas deferens coils 10 times around the testis.

Larvae are in the basal test of specimens collected from Heron I. in June, September, October and December. The trunk is about 1mm long, with the tail wound only about halfway around it. Two adhesive organs are in the anterior mid-line, 3 or 4 epidermal ampullae are along each side, and sometimes there is an additional median dorsal one. The oozooid is well formed, with the thorax protruding separately up into the larval test. Algal cells adhere to the larval test around the posterior end of the trunk around the base of the tail. As the tail straightens, its proximal end (in the haemocoelic cavity) is drawn down, a concavity — the incipient common cloacal cavity — is formed in the larval test above the base of the tail, and the *Prochloron* cells clustered there are drawn in. The larvae probably are free swimming for a short time, one being found in the process of metamorphosis even before its release from the parent colony.

REMARKS. The species is similar to *T. cyclops* in its endostylar pigment cap, sessile atrial aperture across the dorsum and 2 larval adhesive organs. However, it is distinguished by its thin sheet-like colony with black pigment outlining its margin, larger zooids, retractor muscle from the pyloric end of the long oesophageal neck, 10 (rather than 6) coils of the vas deferens, large larval trunk with 3 or 4 (rather than 2) epidermal ampullae per side and *Prochloron* adhering only to the posterior end of the larval trunk (rather than all around it).

The larger colonies assigned by Monniot & Monniot (1987) to *T. cyclops* have all the characters of the present species. These authors invoked intraspecific variation to account for the differences observed in their material. However, the presence of 2 distinct species (neither of which is particularly variable) is the explanation for the observed differences.

A circum-oesophageal muscle shown for this species (Monniot & Monniot, 1987, fig. 2D, E) has not been observed in other examined material (Kott, 1980, 1981, 1982a).

Trididemnum pigmentatum sp. nov.
(Figs, 129D-F, 175B; Pl.16H)

Trididemnum cerebriforme: Kott, 1962: 275 (part, specimens from Hervey Bay, Sarina); 1981: 185. Parry, 1984a: 503.
Didemnum ramosum Sluiter, 1909: 63 (part, ZMA TU476.2).

TYPE LOCALITY. Queensland (Heron I., eastern end of reef, low tide rubble fauna, coll. P. Kott, 10.3.93, holotype QM G308134; Lizard I. on rubble, 30m near Palfrey I. coll. D. Phillips July 1980, paratype QM GH325).

FURTHER RECORDS. Western Australia (Kimberley, WAM 771.91; Montebello Is., WAM 955.93). Queensland (Hervey Bay, QM G9279, G9452, G9455, G9460, G300899, G301808; Capricorn Group, QM GH760, GH901, GH904, GH2272, G302080, G302088, G302090, G302201, G302210, G302309, G302430, G302958, G306200, G308036, G308137, G308174, G308178, G308278, G308316, G308329, G308352; Sarina, QM G4934; Lizard I., QM GH2256, G302417, G302422).

PREVIOUSLY RECORDED. Queensland (Hervey Bay; Sarina QM G4934 – Kott, 1962). West Pacific Ocean (Fiji – Kott, 1981). Indonesia (ZMA TU476.2 Sluiter, 1909).

COLONY. Young colonies near low tide level, and on the under surfaces of rubble, are relatively thin sheets, although some ridges and depressions develop at least on some parts of the surface, and rounded to cylindrical protrusions with terminal cloacal apertures may develop between, or along the surface ridges. As colonies grow these protrusions form bridges over some parts of the outer surface and colonies become complex convoluted masses (QM GH325, G302088, G302210). Rubble often is incorporated in the colony. The upper surface has a thin spicule-free layer of bladder cells, more conspicuous around the margins of the colony than on the upper surface. The bladder cell layer is so thin that the large spicules make the surface feel 'raspy'. Branchial apertures are each surrounded by a layer of spicules which look like a flat-topped papilla projecting into the transparent bladder cell layer. Usually spicules are evenly distributed in the colony, except for a thin layer beneath the cloacal cavity in which they are either sparse or often lacking altogether. Spicules are large (to 0.1mm in diameter and sometimes to 0.12mm), distinctly stellate, with 13–15 long, crowded acutely pointed rays in optical transverse section. The ray length/spicule diameter ratio is 0.37 for spicules with the longest rays. In life, colonies are beige to white or cream, usually with symbiotic *Prochloron* and/or

Cyanophyta on the surface making the colonies green and/or prune[R] or auricular purple[R]. These symbionts are not in obligate symbiosis and are readily brushed off. The dark squamous epithelium in the body wall, especially of the anterior part of the zooids appears dark blue in life, but the zooids are otherwise yellowish beneath the dark pigment. The dark zooids sometimes show through the branchial apertures, creating black spots in the surface of the colony or an overall grey colour. In long term preservation colonies become white, and the zooids brownish pink. The common cloacal cavity is 3-dimensional, with deep canals expanding into posterior abdominal cloacal cavities behind the zooids. Common cloacal apertures are usually elevated, and often are large.

ZOOIDS. Zooids are about 1.5mm long, although this varies with contraction. Their shape also is variable. Sometimes branchial apertures are large and funnel-shaped with the 6 lobes around the rim being short and sharply pointed. Sometimes the ventral lobe is longer and more pointed than the others. In other zooids (even from the same colony) the siphon is relatively short and the lobes more rounded. The atrial aperture is on a short siphon directed posteriorly from the posterior third of the dorsal surface of the thorax. Sometimes 5 minute pointed lobes can be seen around the rim of the aperture. In freshly preserved material the anterior part of the zooid has darkly pigmented squamous epithelium, the nucleus of each cell being colourless. This dark epithelium is interrupted by the large oval lateral organs on each side of the thorax. The dark pigment sometimes fades from the body wall but tends to persist anteriorly, especially in the tips of the branchial lobes and in a branchial velum at the base of the siphon, long after it has faded from much of the branchial siphon and the anterior part of the thoracic wall. An endostylar pigment cap is in the body wall over the anterior end of the endostyle. A retractor muscle of variable length and thickness projects from the posterior end of the thorax.

In the branchial sac 9 stigmata are in the anterior row, 8 in the second and 6 in the last row. The oesophageal neck is relatively short. The distal part of the gut loop is bent ventrally over the large hemispherical testis, around which the vas deferens coils 8 times.

Larvae in the basal test of colonies from Hervey Bay in November (QM G9460); Sarina in August (QM G4934), Heron I. in January (QM GH2272) and March (QM G308174, G308178) and Lizard I. in July (QM G302422) have a trunk only 0.6mm long with the tail wound about two-thirds of the way around it, 4 or 5 pairs of ectodermal ampullae and 2 or 3 antero-median adhesive organs — the second and third adhesive organs sometimes arising from a common basal stalk. Tips of the ampullae are flattened and an arc of columnar cells is along their outer margin.

REMARKS. Like *T. sibogae* and *T. nobile*, this species sometimes develops complex, convoluted colonies with 3-dimensional cloacal canals, zooids with dark squamous epithelium over the body wall, an endostylar pigment cap, a large lateral organ, a retractor muscle from the posterior end of the thorax and 8 coils of the vas deferens. *T. sibogae* has the same number of larval ampullae, and large spicules with long pointed rays, but the spicules have fewer rays. Both *T. sibogae* and *T. nobile* have more variation in spicule distribution — *T. sibogae* sometimes has a patchy distribution of spicules and *T. nobile* can be completely aspicular. *T. nobile* is temperate while the present species and *T. sibogae* are recorded from Indonesia, northern Australia and the tropical Western Pacific

Thick pigmented layers of bladder cells in the surface and base of the colony distinguish *T. savignii* and *T. areolatum*.

Both *T. vahaereere* Monniot & Monniot, 1987 and *T. tomarahi* Monniot & Monniot, 1987 from French Polynesia, have the same distribution of pigment as some of the preserved colonies, and the colonies have the same appearance — the black squamous epithelium in the branchial siphons showing through the layer of similar white stellate spicules in the surface test. Both these species have smaller spicules (to 0.06mm diameter), although *T. tomarahi* has a similar larva with 4 pairs of ectodermal ampullae.

T. spongia Monniot, 1991 is like the present species but its larvae are larger (trunk to 0.09mm long), and it has smaller spicules with fewer rays.

The spicule free layer of test just beneath the posterior abdominal common cloacal cavity is an unusual feature of this species.

Trididemnum pseudodiplosoma (Kott, 1962)
(Fig. 130)

Didemnum pseudodiplosoma Kott, 1962: 321; 1998: 83.

NEW RECORDS. South Australia (QM GH3818).

PREVIOUSLY RECORDED. South Australia (Port Noarlunga, holotype AM Y1527, paratype AM Y1526).

COLONY. Colonies are soft, fleshy, translucent, gelatinous sheets, to complex 3-dimensional masses, with parts of the surface overgrowing and fusing with other parts, (enclosing external surfaces lined with branchial apertures) and sometimes forming lobes or flaps with zooids opening all around the outer surface. The common cloacal cavity is at oesophageal and abdominal levels. The newly recorded colony is completely aspicular, although small (to 0.03mm diameter) burr-like spicules were detected in the thick basal test of the holotype.

ZOOIDS. Zooids are of moderate size (to 1.5mm long). The branchial siphon with 6 pointed lobes around the rim sometimes is goblet-shaped when the circular muscles around its basal half are contracted. The atrial aperture, sometimes with its rim produced into an anterior and a posterior lip, projects on a short siphon from the postero-dorsal corner of the thorax. A fine, tapering retractor muscle projects from the anterior part of the relatively long oesophageal neck. Up to 12 fine, parallel thoracic muscles extend down the length of the parietal thoracic wall; and are crossed by a few fine transverse muscles. The usual bands of transverse muscle fibres are present between the rows of stigmata in the pharyngeal wall. Up to 10 stigmata per row are in each of 3 rows in the branchial sac. About one-third of the length of the pharynx in front of the stigmata is imperforate.

The gut is relatively narrow and forms a long, curved loop. The post-pyloric part is divided into a long cylindrical duodenum, a thick-walled posterior stomach in the pole of the gut loop and a long rectum narrowing in its distal two-thirds. A large almost spherical testis with 8 coils of the vas deferens is beneath the ventral flexure of the gut loop.

Embryos and well advanced larvae are present in the basal test of the newly recorded colony. They are large, the larval trunk is 1.2mm long, and almost spherical with an inflated appearance, the thick test being tightly packed with large bladder cells. The adhesive apparatus occupies the anterior half of the larval trunk. It consists of 3 narrow-stalked, tulip-shaped antero-median adhesive organs, and a circle of 16–24 club-shaped lateral ampullae with long narrow stalks tapering to their base and becoming thicker terminally where their inflated tips are more or less spherical. Sometimes these tips appear to be bilobed (possibly because they have become flattened). The narrow proximal parts of the ampullae originate from a small area in front of the small spherical remnant of yolk and they diverge slightly toward the anterior end of the trunk, forming a corolla around the stalks of the adhesive organs. An oozooid is just behind the middle of the trunk and an arc of up to 6 thoracic buds circles the larval trunk progressively from the left side of the oozooid and anticlockwise toward the ventral part of the right side. The oozooid has a vertical gut loop and abdominal buds project horizontally from its right side. Both oozooids and all the thoracic blastozooid buds have 3 distinct rows of stigmata.

REMARKS. Larvae described by Kott (1962) have been re-examined and are less mature than those of the present colony, having fewer blastozooids and fewer and shorter lateral ampullae. Kott (1962, fig. 47) erroneously showed 4 rows of stigmata in the blastozooid and reported the same number in the zooid. In each case only 3 rows are present. Although the long anterior imperforate area of the pharynx may be mistaken for a row of stigmata, 3 rows of stigmata in oozooid and blastozooids, retractor muscle, conspicuous parallel parietal longitudinal muscles, and posteriorly oriented atrial siphon indicate a *Trididemnum* sp.

The characteristics of the present species are its aspicular test, narrow zooids with a posteriorly oriented atrial aperture (like others in the *savignii* species group but lacking an endostylar pigment cap) and large larvae with prolific development of larval blastozooids, relatively numerous long lateral ampullae forming a corolla around the antero-median adhesive organs and larval test packed with bladder cells.

No other species of *Trididemnum* is known to have larval blastozooids. The number of blastozooids also is unusually high, for only a single blastozooid occurs in relatively few species of *Didemnum* and 2 or 3 at most in *Polysyncraton*, *Lissoclinum* and *Diplosoma*. *Clitella* larvae also have a large number of blastozooids, but its affinities are with *Lissoclinum* rather than *Trididemnum*.

Didemnum effusium, an aspicular species from Queensland, differs from the present one in its generic characters, lack of the turgid bladder cells in the larval test, large, sessile atrial aperture and a thoracic cloacal cavity. *Didemnum jedanense* sometimes is aspicular and its larvae are not dissimilar from the present ones, but it is distinguished by its generic characters, colony form and fewer blastozooids.

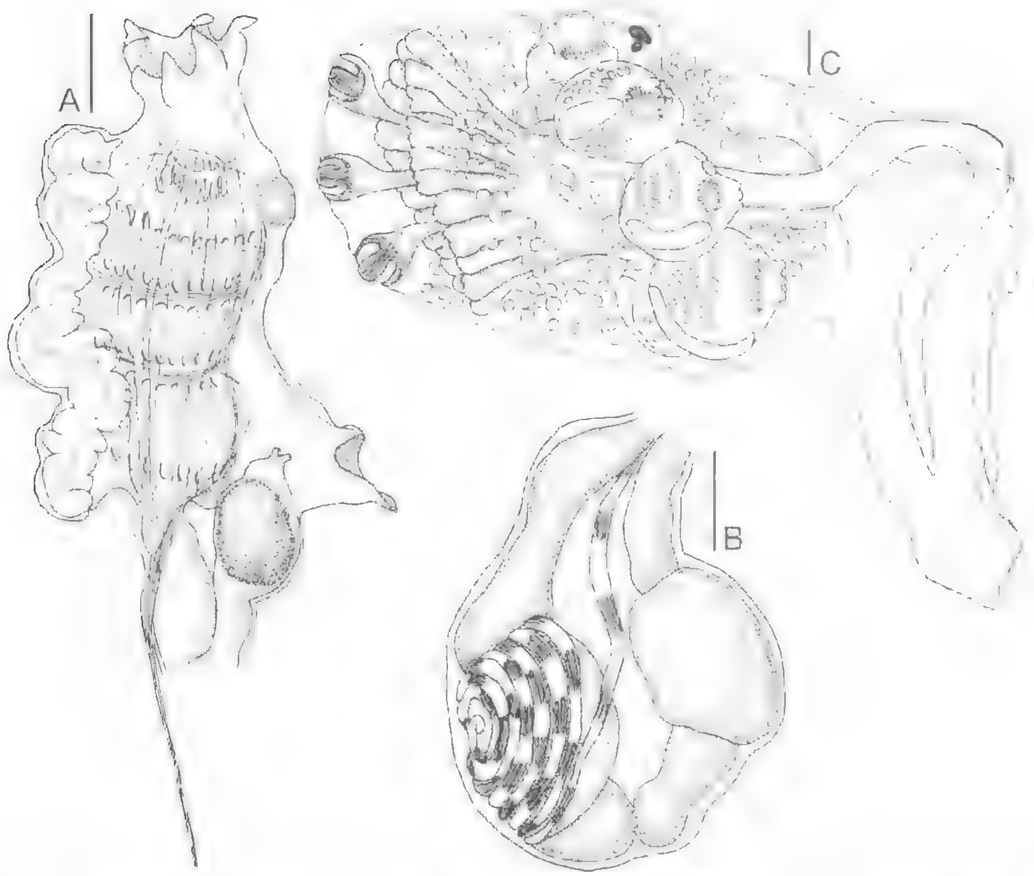


FIG. 130. *Trididemnum pseudodiplosoma* (QM GH3818) – A, thorax; B, abdomen; C, larva showing some of the bladder cells that pack the larval test. Scales: 0.1mm.

Trididemnum savignii (Herdman, 1886)
(Figs 131, 175A; Pl. 17A)

Didemnum savignii Herdman, 1886: 261. Van Name, 1902: 358.

Trididemnum savignii Van Name, 1921: 314; 1924: 23; 1945: 100.

Not *Trididemnum savignii*: Hastings, 1931: 91 (<*T. areolatum*). Pérès, 1949: 184 (part); 1951: 1056. Tokioka, 1953: 197; 1967: 87 (?<*T. tomarahi*). Eldredge, 1967: 178 (?<*T. tomarahi*).

?*Didemnum tenebricosum* Sluiter, 1909: 48.

NEW RECORDS. Northern Territory (Darwin, QM G302918, G303254). Western Australia (Nares Rock, 21 25.8S 115 17.7E, QM G300965). Queensland (Heron I., QM G308288; Lizard I., QM GH329, G302436).

PREVIOUSLY RECORDED. Indonesia (Sluiter, 1909). West Indies, Florida, Bermuda (Van Name, 1902, 1921, 1924, 1930, 1945).

The species is one of the few didemnids with an apparently pantropical range.

COLONY. Colonies are large and fleshy, to 3.5mm thick, with a smooth slippery surface. They are black in preservative, owing to the irregularly shaped pigment cells amongst the crowded bladder cells in the thick superficial layer of bladder cells, which is up to a quarter of the thickness of the colony. Zooids are withdrawn from the surface into a central layer that is about half the thickness of the colony, spicules are in the upper half of this central part at thorax level, although occasionally they are in a thin, crowded layer only one spicule thick immediately beneath the bladder cell layer. Apart from a thick layer on the base of the colony, spicules are absent from the lower half of the colony, which is crowded with bladder cells and black pigment particles as in the upper layer. Some specimens (QM G302918, G303254) have oval faecal pellets embedded in the basal layer of test, sometimes immediately beneath the cloacal cavity. Common cloacal canals run through the test at oesophageal level, sometimes at abdominal level, and occasionally posterior abdominal level, and always beneath the layer of spicules. Large

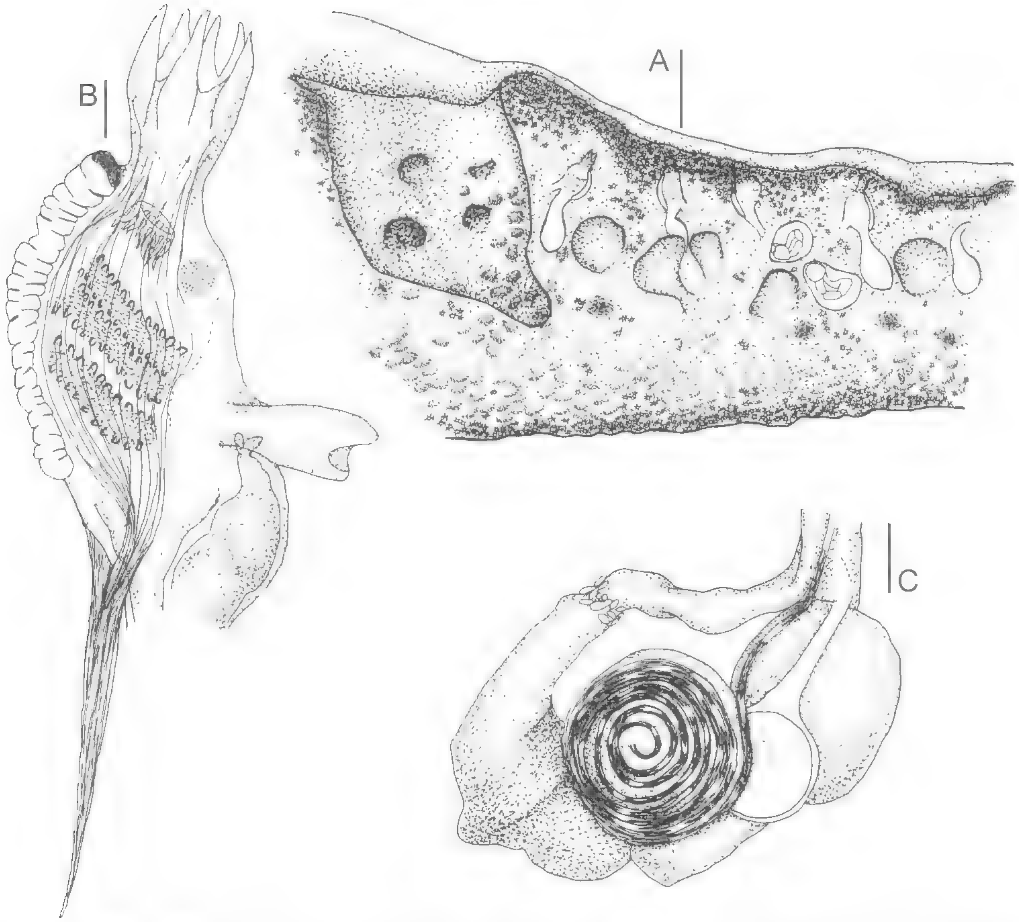


FIG. 131. *Trididemnum savignii* (A,C, QM G303254; B, QM G302436) – A, semidiagrammatic vertical section through colony, showing distribution of spicules, zooids and posterior abdominal cloacal cavities; B, thorax showing endostylar pigment cap; C, abdomen. Scales: A, 1.0mm; B,C, 0.1mm.

spherical black vesicles are in the basal quarter of the colony.

Spicules are large, to 0.13mm in diameter, with 9–13 very tapered, acutely pointed, spiky rays in optical transverse section and ray length/spicule diameter ratio about 0.35.

ZOOIDS. Zooids are large to about 2mm long, thorax, oesophageal neck, and distal part of the abdomen each about one-third. The gut loop always is vertical. The branchial siphon is large, probably contracted in these zooids, with 6 sharply pointed to rounded lobes around the rim of the aperture. The short atrial siphon projects laterally from the posterior end of the dorsal border of the thorax. About 16 fine longitudinal muscles are in the parietal thoracic body wall. A conspicuous retractor muscle of variable length and thickness projects from the postero-ventral end of the thorax. Darkly pigmented squamous epithelium is over the body wall of both thorax and abdomen, although the pigmentation is especially intense at the anterior end of the zooid and on the branchial siphon. An endostylar pigment cap is present.

Twelve stigmata are in each of the 2 anterior rows and 10 in the posterior row of the branchial sac. The gut has the usual divisions, with a marked constriction in the rectum about one-third of the way along the ascending limb of the gut loop. This constriction is surrounded by tubules of the gastro-intestinal gland. Eight coils of the vas deferens surround the undivided testis follicle. Larvae are not known.

REMARKS. Spicules of the newly recorded specimens are larger than those figured by Herdman (1886, pl. 34-4) for *T. savignii*, which

appear to be about 0.03mm diameter. However the scale given by Herdman is imprecise and he may have figured only a moderate sized spicule. The spicules all have similar sharply pointed rays. Like *T. areolatum*, *T. savignii* has a thick surface bladder cell layer, but it is distinguished from that species by its sharply pointed spicule rays and by the spicule distribution — above the cloacal cavity and not in a layer beneath it. *T. savignii*: Hastings, 1931 has both the blunt spicule rays and the thin layer of spicules beneath the cloacal cavity that is characteristic of *T. areolatum*. *T. savignii* of Tokioka (1953: from Japan), Tokioka (1967: from the central and western Pacific and Japan) and Eldredge (1967: from Hawaii) have colonies, with a thin bladder cell layer, spicules scattered throughout rather than being confined to a layer beneath the bladder cells as in *T. savignii* or in a horizontal layer through the middle of the colony as in *T. areolatum* and their spicules are smaller (only 0.06mm in diameter). The Japanese material has smaller spicules with relatively few rays and does not appear to be conspecific with the other specimens

T. natalense Michaelsen, 1920 has been considered a synonym or at least closely related by Van Name (1945), Kott (1962) and Eldredge (1967). Although it has bladder cells superficially and in the basal test, *T. natalense* has a layer of spicules beneath the cloacal canals and this, together with its smaller spicules (to 0.06mm diameter), distinguishes it.

Specimens recorded by Pérès (1949, 1951) from western Africa, with pointed conical spicule rays to 0.075mm diameter may be related to the present species but probably are not conspecific, differing in their thin bladder cell layer.

Specimens assigned to *T. savignii* from the tropical Atlantic (Van Name 1945, part: specimens with pointed rays under a thick surface layer of bladder cells) do not depart from the western Pacific material in any significant way — the only difference detected is the more numerous coils of the vas deferens (although closer examination of the spicules of the Atlantic specimens might demonstrate a difference). However, at this stage the species apparently is pantropical and the problem regarding the type location of *T. savignii*, which Herdman (1886) was uncertain of, is unresolved. The label data — off the Cape of Good Hope — is marked as doubtful and Van Name (1945) suggested that the specimen possibly came from a station off Bermuda, since material he had examined from Bermuda appears to be conspecific.

D. tenebricosum Sluiter, 1909 from Indonesia, was on re-examination of the lectotype (ZMA TU481) found to be a species of *Trididemnum*. Colonies are thin, investing with an uneven surface marked white points where spicules surround branchial apertures and line the siphons as they penetrate the dark superficial bladder cell layer containing pigment in oval, fusiform or branching cells. Zooids are relatively large (1.6mm long) with dark squamous epithelium on the body wall. Stellate spicules to 0.05mm diameter, with long, pointed arms that break up readily are in a layer beneath the surface and another on the base of the colony. The species may be a synonym of *T. savignii*.

Trididemnum sibogae (Hartmeyer, 1910)
(Figs 132, 175D,E; Pl. 17B–G)

Didemnum sibogae Hartmeyer, 1910: 1489, nom. nov. for *Didemnum ramosum* Sluiter, 1909: 63.
Trididemnum sibogae: Kott, 1998: 92.
Didemnum ramosum Sluiter, 1909: 63 (part, specimens from statn 273). Spoel, 1969: 173.
Leptoclinum ramosum Herdman, 1906: 339.
Didemnum frondescens Hartmeyer, 1909-11: 1450 nom. nov. for *Leptoclinum ramosum* Herdman, 1906: 339 (see Monniot, 1995: 328).
Trididemnum frondescens: Monniot, 1995: 328.
Not *Didemnum ramosum* Gottschaldt, 1898: 647 (<*Leptoclinides ramosum*: Monniot, 1995: 328).
Trididemnum cerebriforme: Kott, 1962: 275 (part, specimens from Bargara and ? NSW); 1972c: 247; 1972d: 47. Monniot, 1991: 518.

NEW RECORDS. Western Australia (off Cape Jaubert, QM G306145). South Australia (off Cape Jaffa, QM GH5442; Port Turton, QM G300935, SAM E2605; Pt Victoria Jetty, SAM E2847; Flinders I. , QM GH2290; Kingston, QM G302875; Kangaroo I., QM G300991). Victoria (Western Port, QM G300971, G300982, G300955, G302904). Tasmania (Swan I., QM G302884; southern Tasmania, QM G302902). New South Wales (Port Hacking, QM GH32; Sydney Harbour, QM G303768; Arrawarra, G302891). Queensland (Fraser I., QM G306264; off Cairns, QM GH794; off Princess Charlotte Bay, QM GH952). Northern Territory (Gulf of Carpentaria, QM G302935, G303519).

PREVIOUSLY RECORDED. New South Wales (Port Hacking – AM Z5136-7 Kott, 1972c). Queensland (Bargara – Kott, 1962). Northern Territory (Gulf of Carpentaria – Kott, 1972d). New Caledonia (Monniot, 1991). Indonesia (lectotype ZMA TU476.3, paralectotype ZMA TU1271, Sluiter, 1909). India (Gulf of Manaar, Herdman, 1906).

The species is said to be common at the South Australian, Victorian and Tasmanian locations at which it was sampled.

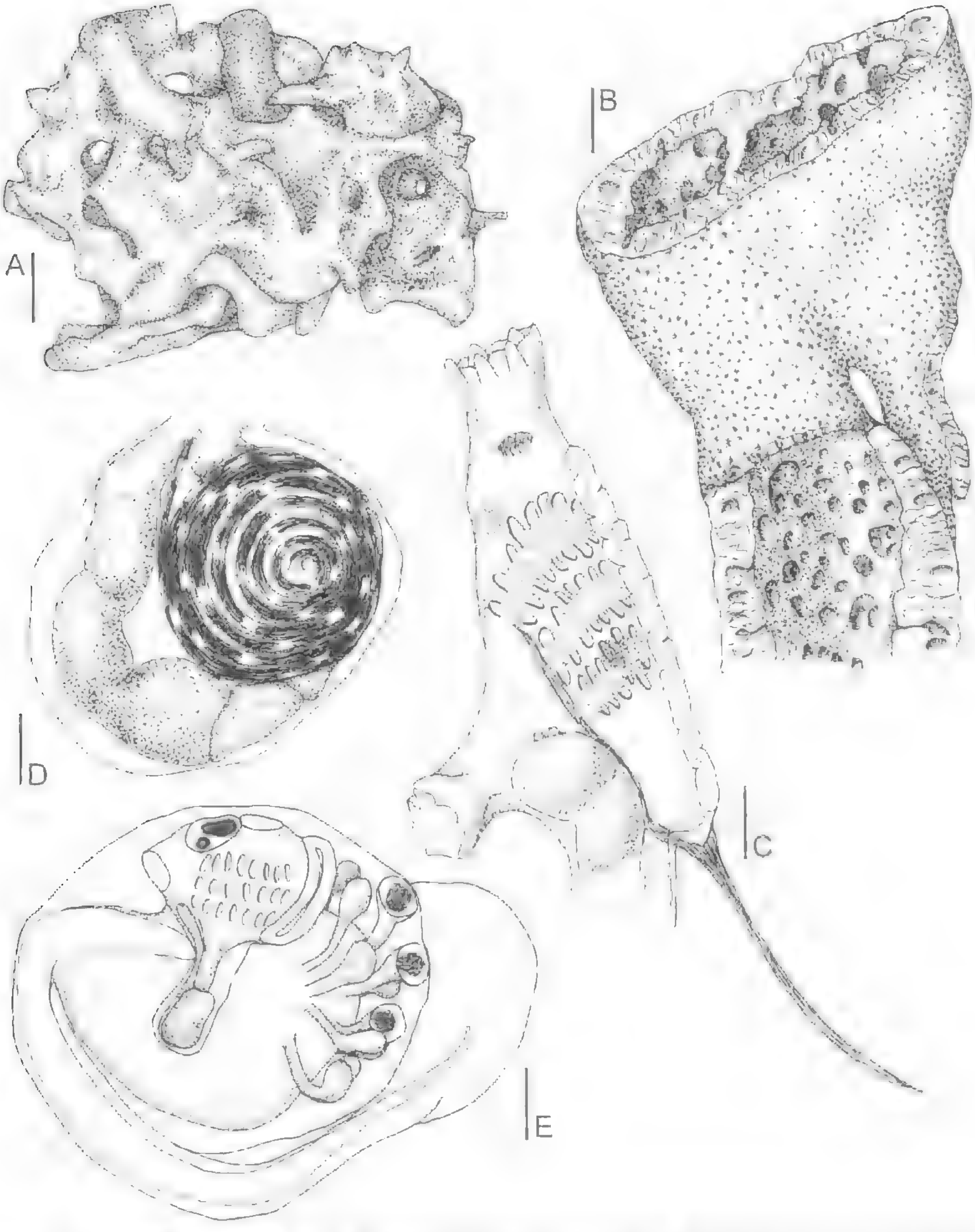


FIG. 132. *Trididemnum sibogae* (A, QM G300955; B, QM G303768; C,E, QM G303519; D, AM Z5137). A, colony; B, semidiagrammatic horizontally sectioned portion of colony with part of one side removed to show common cloacal cavities and zooids; C, thorax; D, abdomen; E, larva (QM G303519). Scales. A, 3.0mm; B, 1.0mm; C–E, 0.1mm.

COLONY. Basically, colonies of this species, which has such great variation in external appearance, are curved, branching vertical lamellae which unite with one another here and there, including fusing across the top of the colony, leaving gaps of various sizes and shapes (but never circular) that lead into internal spaces (or vestibules) enclosed by the branching and

fusing of the primary lobes or lamellae. Accordingly, when the upper margins of the lamellae are more or less entire, the surface may appear to have rounded intertwining ridges, but, when they are firmly joined to one another, the outer surface of the colony tends to be even, often smooth and interrupted only by the irregular gaps between the lamellae, and by the large circular common cloacal apertures (which have clear spicule-free translucent rims that protrude along the top of the ridge and look like sponge oscules. Occasionally swellings develop on the surface and the common cloacal apertures become terminal. Other ornaments on the surface of the colony include pointed tubercles, or minute spicule-filled papillae and/or angular ridges. The shape of these colonies (to 20cm in diameter) is sometimes irregular, often hemispherical and occasionally spherical.

Vast posterior abdominal common cloacal spaces often separate the central test core from an outer zooid-bearing layer. Occasionally the posterior abdominal cloacal spaces occupy most of the core of the colony and only traces of the central core remain as connectives to the internal wall of the outer layer, which is perforated by irregular openings from the thoracic component of the 3-dimensional common cloacal cavities. The intra-colony cloacal spaces together with the vestibular cavities enclosing parts of the outer colonial surface result in very complex sponge-like masses. The surface test is relatively thick. Branchial openings are conspicuously stellate with spicules outlining their margins.

Spicules are stellate (to 0.16mm diameter) with 7–11 long, acutely pointed spiky rays. Ray length/spicule diameter ratio is 0.35–0.4.

Living colonies are black to grey mottled with white or brick colour or yellowish white, the surface colour extending into the linings of the vestibules. Colonies without spicules in the surface are darker grey to black owing to the dark coloured zooids showing through the test, and rarely (SAM E2605) there are aspicular colonies and these are dark throughout. Colonies with spicules lining the common cloacal spaces as well as those with spicules throughout have white lining the cloacal spaces. Often different parts of the colony are different colours merging from dark bluish grey to light grey, brick coloured or yellow. Some living colonies were said to be yellow (QM GH32, G300982), some grey (QM G300971) and others light brown and white (QM G302884). Monniot (1991) recorded living specimens as grey-green, grey-blue, yellow, clear with brown, and intense blue. In preservative the colonies are grey or white and opaque, owing to black pigmented zooids showing through the crowded spicules.

ZOOIDS. Zooids usually have black squamous epithelium in the body wall, especially anteriorly where it obscures the endostylar pigment cap. However, although a small amount of black pigment is in the tips of the branchial lobes, black squamous epithelium and endostylar pigment caps were not detected in some of the colonies from South Australia, Victoria, and Tasmania. The branchial siphon is robust with 6 well-formed pointed lobes and is about one-third of the length of the thorax. Thoraces also are robust, with a short, thick to fine and tapering retractor muscle at the posterior end, a large saucer-shaped lateral organ on each side and a posteriorly oriented atrial siphon. Up to 10 stigmata per row are in the branchial sac, and the vas deferens coils 8 times around the undivided testis. Larvae are being incubated in the central test of specimens taken from the Gulf of Carpentaria (AM Z5136, QM G303519) in November, Port Hacking (QM GH32) in June, and Western Port (QM G300982), Kingston (QM G302875) and Tasmania (QM G302884) in February. They have a trunk 0.7–0.75mm long with 4 ectodermal ampulla on long, slender stalks along each side of the 3 antero-median adhesive organs. The distal tip of each ampulla expands to a curved paddle-shape, concave on the inner surface and convex on the outer surface. The tail is relatively short, wound halfway around the trunk.

REMARKS. The colonies, zooids and larvae, resemble *T. nobile* and *T. vermiforme*. Their ranges overlap in South Australia and Victoria but the present species is the only one with a primarily tropical range. It has larger spicules than the 2 temperate species, 4 larval ectodermal ampullae on each side (rather than 3), and 8 coils of the vas deferens (rather than 10). Like the present species, *T. pigmentatum* is tropical and has large spicules but they have more and longer more pointed rays, the larvae are smaller and the species does not extend into temperate waters. Both *T. savignii* and *T. areolatum* have 3-dimensional cloacal systems and large spicules confined to a single layer beneath a thick superficial layer of bladder cells but their colonies are not complex like the present species. In the former species the rays are sharply pointed but shorter and in the latter they are more

numerous, not so pointed and very much shorter. Although the spicules are not described, *T. cerebriforme*: Monniot, 1991 has similar sized larvae and 4 pairs of lateral ampullae and appears to be conspecific with the present species. *T. cerebriforme* Hartmeyer, 1913 from South Africa has a thin superficial layer of bladder cells and the related species from New Zealand (*T. cerebriforme*: Michaelsen, 1924) has a thicker layer. The South African species has smaller spicules and they are sparse or absent from the deeper parts of the colony (Millar, 1955). *T. spongia* Monniot, 1991 has similar colonies and spicules but a larger larval trunk and 6 rather than 4 larval ectodermal ampullae.

T. lapidosum has similar spicules although they are crowded in the central test core and their rays are not so spiky. Other differences are in the colony and zooids which distinguish the species.

Spoel (1969) designated a lectotype of *D. ramosum* Sluiter, 1909 from Siboga Station 273 (ZMA TU476.3) and accordingly it becomes the lectotype of the present species. Its characteristic colony forms a 3-dimensional network over *Halimeda*, as does the other colony from this location (paralectotype ZMA TU1271: Spoel 1969, pl. 2, fig. 6) and the holotype of *Leptoclinum ramosum* Herdman, 1906, (pl. 9, fig. 3), an almost identical colony which is conspecific.

D. ramosum Gottschaldt, 1898 is the senior homonym of both *D. ramosum* Sluiter, 1909 (*D. sibogae* nom. nov. Hartmeyer, 1910) and *D. ramosum* Herdman, 1906 (*D. frondescens* nom. nov. Hartmeyer, 1910). Gottschaldt's species, though described with 3 rows of stigmata, was found to be *Leptoclinides* (see Monniot, 1995). The name *T. sibogae* is retained for the *Trididemnum* species, although *T. frondescens* has page priority.

Sluiter (1909) assigned another specimen (ZMA TU476.1) from Statn 37, Sailus) to this species, but recognised that its black-rimmed cloacal apertures were atypical. Apparently it had dark squamous epithelium and probably is a *Trididemnum*. On re-examination its spicules appear to be similar to the present species but smaller, and the cloacal cavity is thoracic. The zooids are contracted and its identity is not resolved. A second paralectotype (ZMA TU476.2) of *D. ramosum* Sluiter is conspecific with *T. pigmentatum*.

Although some colonies of *D. psammatode* have lobed and complex colonies, Eldredge (1967) was incorrect in his suggestion that it is a possible synonym of the present species.

Trididemnum spumosum sp. nov.
(Fig. 133A–D, 173F; Pl. 17H)

TYPE LOCALITY. South Australia (Yorke Peninsula, Edithburgh, on Posidonia 3-4m, coll. K.L. Gowlett Holmes 6.1.94, syntypes SAM E2616 photo PE 0320).

COLONY. The very soft, elongate, irregular cushions, to 5cm long, with the upper surface raised into a long ridge, are light green to grey and slightly translucent in preservative. Spicules are very sparse, but evenly distributed throughout, coming to the surface around the branchial siphons, surrounding the apertures and continuing into the siphonal linings to outline the stellate branchial apertures. Branchial apertures, evenly spaced along both sides and on the top of the ridge, are interrupted where common cloacal apertures are raised above the surface on long, chimney-like cylindrical protuberances. Smaller colonies have a single central common cloacal opening, and larger colonies have up to 4 along the upper surface and the colonies are slightly constricted between the openings. This may indicate the initiation of lobulation. Zooids are embedded in the surface layer of test surrounding a vast internal cloacal chamber which is traversed only by thick connectives between the surface test and the thin basal layer.

Spicules are diverse being either burr-like or globular. Both types are particularly small, to 0.02mm in diameter. They have either 7–9 straight rod-like rays in optical transverse section or more numerous, needle-like rays with pointed tips.

ZOOIDS. Zooids are small with a short branchial siphon and a posteriorly oriented atrial siphon. Black squamous epithelium is present over the anterior part of the thorax, although it is faded in some colonies. A short retractor muscle projects from the anterior part of the oesophageal neck. Eight stigmata are in the anterior row, 7 in the second and 6 in the posterior row. Oesophageal buds are present in these zooids, but gonads were not detected. Larvae are not known.

REMARKS. These translucent colonies resemble *Prochloron-Diplosoma* symbioses, although their green colour is in the test and does not appear to be caused by symbionts.

The black squamous epithelium and posteriorly oriented atrial siphon together with the 3 rows of stigmata confirm the generic assignation of this unusual *Trididemnum* sp. Chimney-like projections raising the common cloacal apertures off the surface (where the excurrent water is entrained away from the colony) occur also in cushion-like

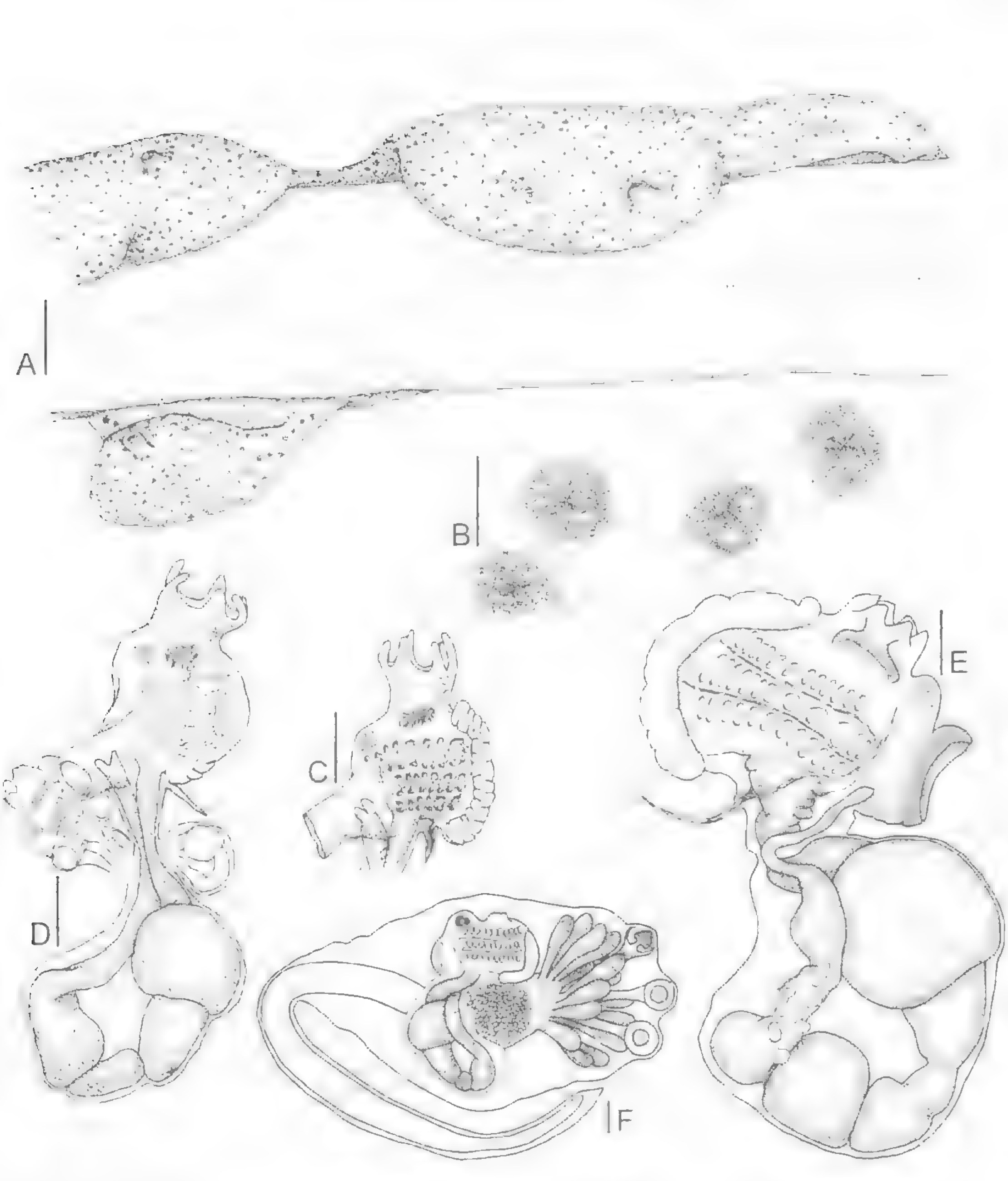


FIG. 133. A–D, *Trididemnum spumosum* sp. nov. (SAM E2616) – A, colony growing along seagrass blade; B, branchial apertures showing distribution of spicules; C, zooid in vegetative phase; D, thorax. E, F, *Trididemnum tectum* sp. nov. (SAM E2834) – E, zooid; F, larva. Scales: A, 3.0mm; B, 0.3mm; C–F, 0.1mm.

colonies of certain tropical species. (see Kott, 1989).

Sparseness of the spicules resembles certain specimens of *T. nobile* which often are aspicular. The colonies are different and appear to lobulate as they grow rather than forming the complex 3-dimensional colonies of *T. nobile*. Also, the spicules are minute, in contrast to the large stellate spicules in the latter species.

The species most closely resembles *T. pseudodiplosoma* having similar burr-like and globular spicules. Distinguishing features are the small colonies, dark squamous epithelium and posterior abdominal cloacal canals. Further, in *T.*

pseudodiplosoma spicules, when present, are in the basal test while in the present species they are evenly distributed throughout.

Trididemnum tectum sp. nov.
(Fig. 133E,F)

TYPE LOCALITY. South Australia (Nuyts Archipelago, Franklin I. NW of West I. intertidal rock pools, coll. W. Zeidler et al., 24.2.83, holotype SAM E2834).

COLONY. The holotype colony is a narrow cushion 3cm long and up to 1cm wide across the upper surface. The test is firm, gelatinous and translucent, white spicules being seen through it. About 3 randomly distributed large sessile common cloacal apertures are on the surface of the colony. The common cloacal cavity forms deep spaces around clumps of zooids and shallow canals penetrate in amongst the zooids in the clumps. Spicules are soft, flexible and readily mutilated, generally small, but spicules to 0.08mm in diameter occasionally occur. They are burr-like to globular, the largest have about 20 conical pointed rays in optical transverse section. They occur in a single layer in the floor of the common cloacal cavity.

ZOOIDS. Zooids are relatively large, probably about 2mm long when relaxed, although examined zooids are contracted. Branchial siphons are well-formed, with 6 pointed lobes around the rim of each opening. Atrial apertures are on robust posteriorly or laterally oriented funnel-shaped siphons. The retractor muscle is short, thick and contracted and projects from the anterior part of the oesophageal neck.

A short stolonic vessel projects from the ventral (concave) side of the gut loop. The thorax is particularly wide with about 12 stigmata in the anterior row and about the same number in the other rows. The gut is thick and robust, and is divided into the usual parts — spherical stomach, duodenum, posterior stomach and rectum. The post-pyloric part of the loop is curved ventrally. The large undivided testis has 6 coils of the vas deferens around it. Embryos are being incubated in the basal test, and larvae probably are released through the common cloacal cavity. The trunk is 1.4mm long with the tail wound only about one third of the way around it. The oozooid has 3 distinct rows of 12 stigmata per row. A conspicuous spherical yolk mass is in front of the vertical gut loop of the oozooid. Eight finger-like lateral ampullae are on long, slender stalks each side of the 3 antero-median adhesive organs.

REMARKS. The large zooids, posteriorly oriented atrial siphon, retractor muscle and large larva with a conspicuous anterior spherical yolk mass indicate the generic affinity even though the 3 rows of stigmata in the adult zooids are obscured by contraction. The firm translucent test, soft spicules in a single layer in the base of the common cloacal cavity, large zooids and larvae, short larval tail and relatively numerous lateral ampullae are characteristic. *T. pseudodiplosoma* is a sheet-like aspicular colony from South Australia, distinguished from the present one by its numerous larval blastozooids. Also from South Australia, specimens of *T. nobile* are occasionally aspicular, but the larvae of the present species have more lateral ampullae and spicules, when present, are different.

T. spumosum has similar narrow colonies and burr-like spicules. Although its common cloacal apertures are projecting chimneys while those of the present species are sessile, this could be an environmental response, and does not necessarily imply a species difference. The present species has larger zooids, with about twice the number of stigmata, spicules larger and present only in the base of its less extensive common cloacal cavity (in *T. spumosum* spicules are throughout the colony). The black squamous ectoderm in *T. spumosum* has not been detected in the present species.

Trididemnum tomarahi
Monniot & Monniot, 1987
(Fig. 174H)

Trididemnum tomarahi Monniot & Monniot, 1987: 22.
Trididemnum savignii: Tokioka, 1967: 87 (part, not specimens from Japan). Eldredge, 1967: 178.
?*Trididemnum planum*: Millar, 1963: 703.

NEW RECORDS. Queensland (Heron I., QM G301895, G308241, G308327; Lizard I., QM G302416).

PREVIOUSLY RECORDED. Queensland (?Bowen – Millar, 1963). French Polynesia (Monniot & Monniot, 1987). Philippines, Palau Is (Tokioka, 1967). Hawaii (Eldredge, 1967).

COLONY. Colonies are small cushions to more extensive flat brittle, investing sheets, with spicules throughout. Common cloacal cavities are at oesophageal level, separating the surface from basal layers of test. Zooids are in clumps, anchored to the basal test by a connective that crosses the common cloacal cavity. Generally the common cloacal cavity penetrates amongst the zooids of each clump at thorax level.

Spicules are stellate, rarely to 0.07mm diameter, and mostly 0.06mm. Nine to 11 conical

pointed rays are in optical transverse section, and the ray length/spicule diameter ratio is 0.3 for spicules with the longest rays.

Living colonies are beige to orange with dark zooids. In preservative they become cream to dirty white owing to dark coloured branchial siphons showing between the stellate spicules as well as through the apertures. Bladder cells are not in a layer on the surface of the colony and the crowded spicules cause it to feel raspy.

ZOOIDS. Zooids are small to 1mm long. Anteriorly they are covered with black squamous epithelium which is also in the branchial siphons. Branchial siphons are relatively long, flaring out toward the aperture, which has 6 pointed lobes around its rim. The atrial siphon is directed posteriorly and sometimes is slightly flared with its rim frilled. The black colour persists around the anterior part of the body and is especially intense in the tips of the branchial lobes, and in a velum at the base of the siphon. A dark pigment cap is over the anterior end of the endostyle. A retractor muscle of varying length projects from the posterior end of the thorax. The gut loop has the usual divisions and the undivided testis has 8 coils of the vas deferens around it.

Larvae in the type specimens have a larval trunk 0.8mm long, with 4 ectodermal ampullae each side of the 3 median adhesive organs. The tail is wound halfway around the trunk (Monniot & Monniot, 1987).

REMARKS. The present species together with *T. vahaereere* and *T. pigmentatum*, lacks a thick surface bladder cell layer and has dark zooids showing through the spicules on the surface of the colony. Spicules of *T. pigmentatum* are larger, and have longer and more crowded rays. *T. sibogae* has surface bladder cells and larger spicules.

The present species has spicule rays in polygonal bases (Monniot & Monniot, 1987). They are more conspicuous as a result of the disintegration of the central spicule mass. A similar condition is seen in *T. vahaereere*.

The average size of spicules in the type material is 0.06mm for *T. tomarahi* and 0.065mm for *T. vahaereere* (Monniot & Monniot, 1987). Their maximum size is not known. Spicules described for *T. tomarahi* from French Polynesia resemble both *T. vahaereere* and the newly recorded specimens of *T. tomarahi* in most respects. Variations in zooids, due to age, contraction and preservation make it impossible to sustain differences in pigmentation and proportions of the zooids as species characteristics. The only significant difference between *T. tomarahi* and *T. vahaereere* is the origin of the retractor muscle from the posterior end of the thorax in *T. tomarahi* and from the base of the oesophageal neck in *T. vahaereere*.

T. savignii: Tokioka, 1967: 80 from the Hawaiian Is and the Philippines and *T. savignii*: Eldredge; 1967 from the western Pacific have a thin bladder cell layer and stellate spicules to 0.06mm diameter with blunted rays scattered throughout the test are not *T. savignii* Herdman, 1886, which has a thick bladder cell layer and sharply pointed spicules in a layer beneath the bladder cells and above the common cloacal cavity. The specimens may be conspecific with *T. tomarahi*. They are different from *T. savignii*: Tokioka, 1953 from Japan, which has much smaller spicules (less than 0.03mm diameter), and may be an undescribed species.

T. planum: Millar, 1963 from Bowen appears to have been incorrectly assigned, having spicules crowded through the test rather than in a single layer.

Spherical cells about 0.02–0.025mm diameter adhering around the outside of some zooids (QM G308327, G308241) may be test cells.

Trididemnum vermiforme sp. nov.
(Figs 134, 174-I; Pl.18A,B)

Trididemnum cerebriforme: Kott, 1962: 275 (part specimens from Phillip I.); 1997: pl. 81(1).

TYPE LOCALITY. South Australia (Beachport Jetty, central South Australia, on jetty piles, coll. AIMS Bioactivity Group 20.2.89, holotype QM G300960); Victoria (Portsea Pier, coll. G. Russ ascidian sp. 29 panel 40.1 24.10.75 to 22.4.76. paratype QM G11925).

FURTHER RECORDS. South Australia (Reevesby I., SAME2602); Victoria (Phillip I. – Kott, 1962; Lorne, AM Y2317).

COLONY. From the surface, these thick, fleshy, encrusting colonies to 7cm or more in maximum dimension look like a mass of intertwining long worm-like tubes about 1cm in diameter. They result from narrow outgrowths overlapping and fusing with other parts of the surface and with one another. Conspicuous circular common cloacal apertures are along the surface of the ridges and sometimes on the tips of the developing lobes. A conspicuous layer of bladder cells is on the outer surface of the colony and a thin rim of spicule-free test surrounds each common cloacal aperture. In the centre of each of the intertwining tubes is a large posterior abdominal common cloacal cavity, and there is no central rod of test.

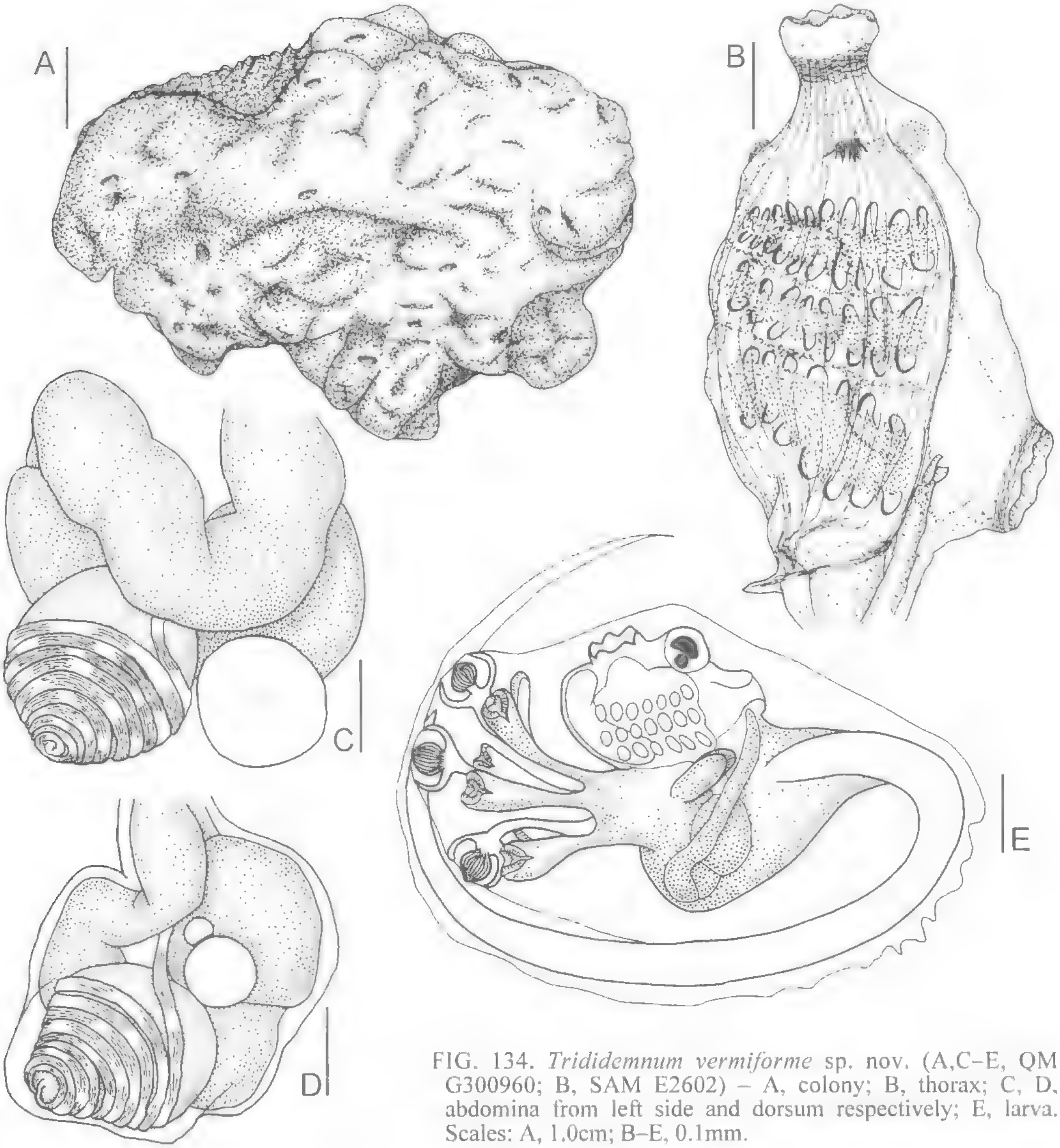


FIG. 134. *Trididemnum vermiforme* sp. nov. (A,C–E, QM G300960; B, SAM E2602) – A, colony; B, thorax; C, D, abdomina from left side and dorsum respectively; E, larva. Scales: A, 1.0cm; B–E, 0.1mm.

The common cloacal cavity extends out toward the surface separating clumps of zooids from one another.

Spicules are in a crowded layer beneath the bladder cells and in an even layer lining the common cloacal cavity. They also are present throughout the rest of the colony although they are less crowded there. They surround the thoraces but are not present over the top of the zooids except for the small groups around each branchial siphon which continue into the siphonal lining. Dark squamous epithelium around the zooids, endostylar pigment caps and black pigment in the branchial lobes cause the living colonies to appear grey or black, although this pigmentation is not present in some colonies or in some parts of a colony and the colour is then cream, the white spicules showing through the bladder cells.

Spicules are large (to 0.09mm diameter) and stellate with 7–9 conical pointed rays. The ray length/spicules diameter ratio about 0.3.

ZOOIDS. Zooids are small, just over 1mm long. The branchial siphon is relatively short with well formed branchial lobes and a short atrial siphon projects posteriorly from the posterior third of the thorax. A large saucer-shaped lateral organ is on each side of the thorax covering the postero-ventral third of the thorax. Anterior to the perforated part of the pharynx, about one quarter of the length of the pharynx is imperforate. Sometimes a very short, rudimentary retractor muscle, consisting of only very few short fibres, projects form the posterior end of the thorax. However sometimes a retractor was not detected at all (QM G300960). The gut forms a tight double loop, and the vas deferens makes 10 spirals around a conspicuously top-shaped testis.

Orange-coloured embryos are crowded in the surface layer of some parts of AM Y2317 collected in November. They are around the common cloacal cavity in the holotype and most probably are liberated through that cavity. The larval trunk is about 0.65mm long and sometimes is quite cigar-shaped. The tail is wound only about half the distance around it. The posterior end of the larval haemocoel is drawn out into a cone around the base of the tail. The oozooid is halfway along the trunk, and its anterior third is occupied by 3 slender ectodermal ampullae along each side of the 3 antero-median adhesive organs. The tips of the ectodermal ampullae are curved, the concavity being on the mesial side. Columnar epithelial cells are along their straight terminal margin.

The paratype colony which is a large slab about 7cm in maximum dimension was taken from an experimental panel deployed 6 months before. Accordingly, its age is 6 months or less.

REMARKS. The species resembles and overlaps the temperate part of the range of *T. sibogae*. It can be distinguished from the latter species by its smaller spicules, absence of an axial test core, narrower colony lobes, smaller and more numerous common cloacal apertures, less robust zooids, shorter branchial siphon, more numerous vas deferens coils and 3 (rather then 4) larval ectodermal ampullae.

The South African *T. cerebriforme* Hartmeyer, 1913 also resembles the present species but is distinguished by its restricted spicule distribution and 4 larval ectodermal ampullae (Millar, 1955). *T. nobile* is also similar in many respects but has thicker colony lobes, smaller spicules, missing from many parts of the colonies, which often are completely aspicular.

Genus **Lissoclinum** Verrill 1871

TYPE SPECIES. *Lissoclinum aureum* Verrill, 1871.

The genus is characterised by a straight vas deferens with the proximal end hooked around a testis that usually is bipartite or undivided, although some, including the type species have a testis of up to 10 follicles (see Van Name, 1945). The branchial sac is large, but delicate, with long, rectangular stigmata in 4 rows. The abdomen is relatively large, the gut loop capacious with a large balloon-like stomach, a moderately long and wide duodenum abruptly constricted from the long oval posterior stomach which also is balloon-like and is in the pole of the gut loop. The distal end of the posterior stomach also is constricted where it meets the rectum (which constitutes the ascending limb of the gut loop). A rectal valve sometimes (*L. nebulosum* Monniot & Monniot, 1996) is present at the junction of the rectum and posterior stomach. Spicules usually are present in the test, being absent only in *L. multifidum* (Sluiter, 1909) and *L. multitestis* Monniot & Monniot, 1996, although many species are partially aspicular and in others spicule distribution is restricted.

As in other genera, body musculature consists of a branchial sphincter, fine longitudinal bands in the parietal body wall, transverse muscles between the rows of stigmata continuing over the mid-dorsal line beneath the pair of dorsal longitudinal pharyngeal muscle bands (relatively fine in this genus), one on each side of the dorsal mid-line. In some species the pharyngeal and parietal longitudinal muscles join those from the opposite side ventral to the oesophageal neck and extend into the test as a short retractor muscle — robust, but never as long as in other genera. As in a few species of *Didemnum* and *Trididemnum*, *L. nebulosum* and *L. roseum* have muscles encircling the oesophageal neck in a wide band rather than forming a retractor muscle. Occasionally a relatively short atrial lip is on the upper rim of the opening but it is not long and forked as in *Polysyncraton*. As in certain *Trididemnum*, *Diplosoma*, *Polysyncraton* and *Didemnum* (see Glossary), *L. variabile* is known to have black squamous epithelum on the abdomen, although it is not on the thorax where crowded columnar cells project from the surface — as they do in *L. nebulosum* and *L. timorense* and in many *Polysyncraton* and *Didemnum* species.

Colonies of *Lissoclinum* are diverse. Some are massive, e.g. *L. patella* is often a metre or more in

maximum dimension. Others are small cushions or plate-like colonies (some obligate *Prochloron* symbioses) known to subdivide (*L. bistratum*, *L. timorense*). Many are thin, soft, film-like, often elastic sheets, usually brightly coloured, with large, sessile common cloacal apertures, and covering areas up to one metre. When free from the substrate, these sheets sometimes retract into thick soft masses (e.g. *L. badium*). In most sheet-like colonies common cloacal cavities are extensive, zooids being embedded in test connectives that cross the cloacal cavity vertically, connecting surface to basal test. Such colonies look robust in life as they are inflated by water pressure in the common cloacal cavity. In preservative this cloacal cavity collapses.

Spicules often are unusual shapes, such as flattened with rays of unequal length, or tetrahedral to 6-rayed with long, strong points or arms, each formed by a single large ray or made up of a number of particularly long, crowded rays. Spicules often partially or wholly encapsulate the zooids and are absent from other parts of the colony (e.g. many species in the *verrilli*, *triangulum* and *punctatum* species groups).

Embryos sometimes develop in a brood pouch that remains attached to the abdomen of the zooid by a narrow stalk (*L. maculatum* and *L. roseum*) as in *Diplosoma ferrugeum*. Larvae are of moderate size, often with 1 or 2 blastozooids. Although many species have the usual 4 or 5 pairs of lateral ampullae, sometimes (e.g. *L. tasmanense*, *L. sente* and *L. pacificense*) the lateral ampullae are balloon-shaped, with slender stalks and enlarged epidermal cells terminally, and in other species (e.g. *L. bistratum*, *L. timorense*, *L. patella*, *L. textrinum* Monniot, 1992) small sometimes spherical or tear-drop shaped vesicles surround the anterior end of the trunk. The adult organs are better developed in the oozooid than is usual in *Polysyncraton* — the branchial sac and the gut usually being well formed. Unlike *Didemnum* and *Trididemnum*, the larval oozooid (as well as the blastozooid) has 4 rows of stigmata (as in *Diplosoma* and *Polysyncraton*). The oozooid and blastozooids are halfway along the larval trunk, not at its anterior end as in *Diplosoma*.

Lissoclinum larvae often have opaque, sometimes comma-shaped triangular or irregular bodies and sometimes morula cells in the larval test. These have variously been described as pigment cells or spicules or triangular bodies (Eldredge, 1967, Kott, 1962, Monniot, 1992). In *L. tasmanense* they are triangular or comma-shaped bodies in the test over the posterior half of the larval trunk. However in *L. abdominale* Monniot, 1983 (see also Monniot, 1992) similar bodies completely surround the trunk. Granular bodies completely enclose the larvae of *L. fragile* Van Name, 1902 and *L. japonicum* Tokioka, 1958 as well as *L. badium*, *L. caliginosum*, *L. ostrearium*, and *L. regnum* leaving 'windows' over the sense organs and in front of the adhesive organs in the same way as do the symbiotic plant cells around the larval trunk of certain species in obligate symbioses — *Didemnum viride*, *D. poecilomorpha*, *Trididemnum clinides*, *T. cyclops*, *T. miniatum*, *T. paraclinides* and *T. strigosum* (see Kott, 1980, 1982a). In these symbioses the plant cells surround the test of the larval trunk and can be removed, while in *Lissoclinum* the opaque cells are firmly embedded in it. Their nature and role is not known.

Lissoclinum has many species (the number exceeded only by *Trididemnum*) in symbiosis with the prokaryote *Prochloron*. These are *L. bistratum*, *L. patella*, *L. punctatum*, *L. spongium*, *L. triangulum* and *L. timorense*. A phylogenetic relationship may exist between *L. punctatum* and *L. triangulum*, and between *L. bistratum*, *L. spongium* and *L. timorense*, and conceivably the symbiosis could have evolved once only in each of these related groups, and independently in *L. patella* i.e. at least 3 times in this genus. However, more likely it has evolved in parallel in each of the 6 species. Although the symbionts adhere to the test of the posterior part of the larval trunk no particular organ (such as the rastrum in *Diplosoma*, Kott, 1980) has evolved to carry the plant cells from one generation to the other.

The genus resembles *Diplosoma*, differing from it principally in the presence of spicules and in the position of oozooid and blastozooids in the larval trunk — about halfway along it in *Lissoclinum* but anteriorly, immediately behind the adhesive organs in *Diplosoma*. *Echinoclinum* Van Name, 1902, has previously been separated from *Lissoclinum* by its tetrahedral to 6-rayed spicules, and the origin of the vas deferens (which is not hooked around the testis follicle to the same extent as in *Lissoclinum*). These differences do not seem to be of generic significance, so *Echinoclinum* is treated here as a synonym of *Lissoclinum* following Eldredge (1967) and Monniot & Monniot (1987).

Polysoma Kott, 1983 was erected to accommodate spicule-free forms with numerous testis follicles and a straight vas deferens. The zooids resemble those of *Lissoclinum*, of which the type, *L. aureum* Verrill, 1871 has numerous male follicles. *Polysoma* is here regarded as a junior synonym of *Lissoclinum*. The type, *P. testiculatum* Kott, 1983 < *L. multifidum* (Sluiter, 1909), and *L. multitestis* (Monniot & Monniot, 1996) both have a large number of male follicles and lack spicules. *L. cornutum* Monniot, 1992 and *L. polyorchis* Monniot, 1992 from New Caledonia and *L. concavum* rom southern Australia also have numerous testis follicles, but contain spicules.

Michaelsen (1920) interpreted the rather pronounced hook at the proximal end of the vas deferens as an incipient coil. However, it is hooked because it originates at the posterior end of the testis and then bends around the outside (posterior to the zooid if the abdomen is flexed ventrally) to extend anteriorly with the rectum. The hook is emphasised by the flexure of the whole distal part of the abdomen, the vas deferens tending to bend to the left so that it extends across to the left side, rather than the dorsal side of the testis, thus resembling an incipient coil. Characters of both the zooids and the larvae of species examined in the course of this study attest to *Lissoclinum* as a monophyletic genus level taxon separate from the genus *Didemnum*.

Several species groups can be identified in *Lissoclinum*. They are:

1. The *aureum* group, characterised by the division of the testis into a number of separate follicles. Known members of the group are *L. aureum* Verrill, 1871 from the north western Atlantic, *L. cavum* Millar, 1962 from South Africa, *L. cornutum* Monniot, 1992 and *L. polyorchis* Monniot, 1992 from New Caledonia, *L. concavum* from southern Australia, *L. multifidum* (Sluiter, 1909) from northern Australia and Indonesia and *L. multitestis* (Monniot & Monniot, 1996) from the Coral Sea.

2. The *timorense* group has two-lipped branchial apertures appearing as slits on the surface of the colony. Larvae have numerous small stalked vesicles around the anterior end of the trunk. This group contains symbiotic *Prochloron* in vast 3-dimensional common cloacal systems that consist of deep and sometimes posterior abdominal spaces around clumps of zooids. These cavities penetrate the clumps of zooids at thorax level. Species in this group are probably autotrophic, the zooids having short gut loops, and an elaborate arsenal of mechanisms to control the amount of light falling on the symbionts. This includes the rearrangement of spicules in the colony (in *L. timorense* and *L. bistratum*), the development of high ridges of gelatinous translucent test leaving the spicules and zooids in a thin layer about halfway down the thick colony (*L. patella*), the adjustment of carotenoid pigments in the surface test (*L. bistratum*) and the adjustment of chlorophyll a/b ratios in the symbionts (Parry, 1987).

Known members of the group are *L. bistratum* (Sluiter, 1909), *L. timorense* (Sluiter, 1909) and *L. patella* (Gottschaldt, 1898) from the Indo-West Pacific, and *L. spongium* from Lord Howe I.

3. The *verrilli* group, with tetrahedral spicules in which the rays are of different sizes, the longer ones grouped and/or compacted into the long, pointed arms. These species were contained in *Echinoclinum*, here proposed as a junior synonym of *Lissoclinum*. The test in this group of species appears to be always soft and gelatinous, spicules often encapsulate the zooids, and are never found crowded in the colony.

Known members of the group are: *L. calycis* Monniot, 1992 and *L. vulgare* Monniot, 1992 from New Caledonia, *L. pacificense* (Kott, 1981) from Fiji, *L. sente* from Fiji and the western Pacific, *L. taratara* Monniot & Monniot, 1987 and *L. tuheiavae* Monniot & Monniot, 1987 from French Polynesia and the tropical western Pacific, *L. tasmanense* (Kott, 1954) from southern Australia, and *L. verrilli* (Van Name, 1902) from the tropical western Atlantic.

4. The *triangulum* group sometimes have flat spicules with rays of uneven length that are graded to an irregular diamond, triangular or oval outline. Spicules are similar to the *verrilli* group of species although the rays are not consolidated into arms — they remain thin and rod-like and the spicules burr-like as in the *punctatum* and *fragile* groups, although not globular, and the cloacal systems are more restricted. The *triangulum* group may be intermediate between the *fragile* and *punctatum* groups and the *verrilli* group. The spicules sometimes encapsulate the zooids, but the test is firmer than in either the *verrilli* or the *punctatum* groups.

Known members of this group are *L. nebulosum* Monniot & Monniot, 1996, *L. triangulum* (Sluiter,

1909) and the related *L. mereti* Monniot & Monniot, 1987.

5. The *punctatum* group has small spicules, usually burr-shaped, that partially or completely encapsulate the zooids, and extremely soft test that disintegrates into mucus when it is cut. *L. punctatum* is the only member of the group with an obligate symbiosis with *Prochloron*.

Known members of the group, all from the tropical western Pacific, are *L. limosum*, *L. punctatum* Kott, 1977, *L. ravarava* Monniot & Monniot, 1987, *L. roseum* and *L. tunicatum* Monniot & Monniot, 1996.

6. The *fragile* group contains species with a thin colony forming very extensive film-like sheets over the substrate. They contain vast common cloacal cavities that, in the living specimens are kept inflated by the pressure of the excurrent water flowing through them. These cloacal cavities are horizontal, occupying most of the thickness of the colony. The zooids usually are suspended in thin strips of test, either individually or in small clumps of 2 or 3, between the thin surface and basal layers of test. This type of cloacal system is found almost universally in *Diplosoma*. Unlike *Diplosoma*, spicules usually are quite crowded in all layers of the test. Certain members of this group have a single layer of small (about 0.01mm) granular bodies in the test of the known larvae (*L. badium*, *L. ostrearium*, *L. fragile*, *L. reginum*, *L. caliginosum* and *L. maculatum*). In some species dark spherical cells are in the adult haemocoel and in others they are in the test and surround the zooids (see Glossary, **haemocoel**).

Known members of the group are *L. ostrearium* Michaelsen, 1930 from SW Australia, *L. reginum*, *L. badium* *L. vareau* Monniot & Monniot, 1987, *L. maculatum*, *L. caliginosum*, and *L. conchylium* from the tropical western Pacific, and *L. fragile* (Van Name, 1902) from the tropical western Atlantic. Despite their thoracic common cloacal cavities *L. durabile* from southern Australia and *L. conchylium* from the eastern sub-tropics have similar spicule-filled test, large thoraces fixed firmly in the test and dark blood cells in the haemocoel and probably are members of this group.

L. variabile is unusual and has not been placed in any of the above species groups. It has extensive cloacal cavities and thin investing colonies that, like members of the *fragile* group, resemble *Diplosoma* spp. It lacks the burr-like or globular spicules of other species of the *fragile* group, having instead a diversity of spicules including stellate ones with a variable number of rays and others with flattened tongue-like rays (like those of *Polysyncraton pontoniae*). It also is unique in *Lissoclinum*, having black squamous epithelium (see Glossary).

Lissoclinum does not contain a large number of species although it is more diverse in the tropics than in temperate waters. Most species, however, have a wide geographic range.

KEY TO THE SPECIES OF *LISSOCLINUM* RECORDED FROM AUSTRALIAN WATERS

1. Testis follicles 1 or 2 only 2
   Testis follicles more than 2 23
2. Spicules globular, burr-like or stellate, rays of approximately even length 3
   Spicules not globular, burr-like or stellate, rays of conspicuously uneven length 18
3. Spicules only encapsulating zooids; or sparse throughout the colony 4
   Spicules not only encapsulating zooids; present and abundant at one or more levels or throughout colony . 7
4. *Prochloron* present . . . . *L. punctatum*
   Prochloron not present 5
5. Spicules encapsulate zooids; stellate spicules not present 6
   Spicules do not encapsulate zooids; stellate spicules present . . . . *L. variabile* sp. nov.
6. Colony pink . . . . *L. roseum* sp. nov.
   Colony brown . . . . *L. limosum* sp. nov.
7. *Prochloron* in common cloacal cavity 8
   Prochloron not in common cloacal cavity 11
8. Systems of zooids opening into deep pits in thick, gelatinous surface test . . . . *L. patella*
   Systems of zooids not opening into deep pits in thick gelatinous surface test 9
9. Spicule rays mostly flat-tipped, spicules globular; retractor muscle present 10
   Spicule rays not mostly flat-tipped, spicules not globular; retractor muscle not present . . . . *L. timorense*
10. Spicules to 0.05mm diameter. . . . . *L. bistratum*
    Spicules never more than 0.025mm diameter . . . . *L. spongium* sp. nov.
11. Spicule-free superficial bladder cell layer conspicuous . . . . *L. caliginosum* sp. nov.
    Spicule-free superficial bladder cell layer absent or inconspicuous 12
12. Abdomina entirely or at least partially embedded in basal test 13
    Abdomina suspended in cloacal cavity between basal and surface test 15
13. Spicules crowded throughout; spicule rays more than 13 in optical transverse section 14
    Spicules not crowded throughout; spicule rays not more than 13 in optical transverse section . *L. levitum* sp. nov.
14. Common cloacal openings evenly spaced on small conical elevations . . . . *L. durabile* sp. nov.

Common cloacal openings sessile and not evenly spaced . . . . *L. conchylium* sp. nov.

15. Spicules to 0.04mm diameter; with a retractor muscle . . . . *L. reginum* sp. nov.

Spicules not more than 0.03mm diameter; without a retractor muscle 16

16. Colonies small cushions; testis undivided . . . . *L. maculatum* sp. nov.

Colonies thin films; testis 2 follicles 17

17. Spicules mixed with bladder cells in the surface . . . . *L. badium*

Spicules crowded in the surface . . . . . . *L. ostrearium*

18. Spicules flattened, usually encapsulate zooids . . . . *L. triangulum*

Spicules not flattened, sometimes encapsulate zooids . 19

19. Spicule rays separate from one another and never compacted into long arms . . . *L. nebulosum*

Spicule rays of unequal diameter, some compacted into long arms . . . 20

20. Spicules with 4 to 8 long, compacted arms only; no central mass 21

Spicules not with 4 to 8 long compacted arms only; a central mass of separate or compacted rays 22

21. Lateral ampullae in larval trunk 12/side . . . *L. tasmanense*

Lateral ampullae in larval trunk 4/side . . . *L. sente* sp. nov.

22. Spicules with thick, loose rays in central mass . *L. taratara*

Spicules without thick, loose rays in central mass . . . . *L. calycis*

23. Spicules present . . . *L. concavum* sp. nov.

Spicules not present . . . *L. multifidum*

The following species have had Australian or western Pacific specimens assigned to them in error; or have been recorded from adjacent regions, but are not known to occur in Australian waters:

Lissoclinum abdominale Monniot, 1983 from Guadaloupe is said to be conspecific with specimens recorded from New Caledonia (Monniot, 1992). This is unlikely. Neither the opaque triangular cells in the larval test nor the position of the spicules in a plate between the thorax and flexed abdomen are diagnostic features. The former occur in other species (e.g. *L. tasmanense*). The position of the spicules is presumably because they are in the strip of test along the ventrum of the thorax — test being absent from the dorsum where the atrial aperture exposes the pharynx. Although they are said to be spherical (Monniot, 1992), both Atlantic and New Caledonian specimens have spicules with needle-like rays of unequal length like those of *L. ravarava*, with which the Pacific specimens are here regarded as conspecific.

Lissoclinum cornutum Monniot, 1992 from New Caledonia is one of a group of species with follicles arranged in a circle (*L. aureum* group). It has large stellate spicules that distinguish it from other species in the group.

Lissoclinum fragile (Van Name, 1902) is an Atlantic species said to occur in Western Port, Victoria (Kott, 1976), French Polynesia (Monniot & Monniot, 1987) and New Caledonia (Monniot, 1992). The Australian species is discussed below (see *L. durabile*). In the type material, a retractor muscle is absent, and probably an atrial tongue is present. According to Van Name (1902, 1921, 1945) the spicules, rather than being only burr-like with fine needle-like rays, sometimes have flat-tipped and conical rays. The smaller branchial sac, and the absence of pigment in the test that characterises living specimens of the Atlantic nominal species further distinguish it from the Western Pacific *L. fragile*: Monniot & Monniot (1987) and Monniot, 1992 which sometimes has a retractor muscle, usually some pigment, and has only burr-shaped spicules with needle-like rays (see *L. reginum*).

Lissoclinum japonicum Tokioka, 1958 from Japan and the western Pacific (Nishikawa, 1990; Monniot, 1992), like some specimens of *L. reginum* is rose-mauve in life but lacks a retractor muscle, has numerous (6 pairs) larval ectodermal ampullae, and 5 adhesive organs. Unlike *L. conchylium* (which also is blue) it has an atrial tongue and small spicules (not more than 0.03mm in diameter). It is related to *L. badium* from the tropical western Pacific.

Lissoclinum mereti Monniot & Monniot, 1987 from French Polynesia closely resembles *L. triangulum* in its flattened spicules and undivided testis but has larval blastozooids and 4 (rather than 6) pairs of larval ampullae.

Lissoclinum multitestis (Monniot & Monniot, 1996) from the Coral Sea SW of Port Moresby is distinguished from *L. multifidum* Sluiter, 1909 by its larger zooids (3mm long) more stigmata (25 per row), gastric vesicle between the tubules of the gland and the duct, absence of a retractor muscle, and large (2mm long trunk) larva which, however, lacks blastozooids.

Lissoclinum notti Brewin, 1958, from Hauraki Gulf, North I., New Zealand forms thin violet to brown encrusting colonies. Spicules (to 0.04mm with rather irregular flat-tipped rays) are crowded in surface and base, but not between. The testis is undivided. The ovary is in a sac constricted off from the abdomen. The common cloacal cavity is the depth of the whole zooid. A retractor muscle is not recorded, but an atrial tongue is present. *L. variau* Monniot & Monniot, 1987 is similar although it has 10 pairs of larval epidermal ampullae, while *L. notti* has 4 pairs. *L. reginum* has some characters of *L. notti*, including its blue colour, and similar sized spicules, but it has a retractor muscle and the spicules have flat-tipped rather than the irregular rays they have in *L. notti*. There are 2 known temperate Australian species with which *L. notti* could be confused. *L. durabile* has a more restricted cloacal cavity than the New Zealand species, and *L. ostrearium*, has smaller spicules. Both have 2 rather than one testis follicle.

Lissoclinum pacificense (Kott, 1981) from Fiji, has a large larval trunk (1.2mm long) like *L. tasmanense*, but only 6 pairs of balloon-like spherical larval lateral ampullae. The spicules have 5–7 long compact arms with a tuft of short, needle-like rays in the centre (0.06mm between tips of adjacent arms). Larvae are large (trunk 1.2mm long), with 5 rounded terminal ampullae on narrow stalks along each side of the 3 antero-median adhesive organs, and 2 blastozooids. Specimens originally assigned to *L. pacificense* included one (QM GH59) from Dravuni

and another (QM G9467) from Heron I. which have spicules with long pointed arms, but lack the central needle-like spines. This is a separate species (*L. sente*). Monniot & Monniot (1987), in discussing *L. verrilli* (Van Name, 1902) confused *L. pacificense* with *L. philippinense* (Tokioka, 1967), a synonym of *L. triangulum* (Sluiter, 1909), as shown by Kott (1980), who examined the types of the former species (USNM 11790-1). *L. pacificense* has spicules like, but smaller than, *L. tuheiavae*.

Lissoclinum polyorchis Monniot, 1992 from New Caledonia is a member of the *aureum* group with a number of testis follicles arranged in a circle. It is distinguished by its diverse spicules, some with polygonal bases, in which the tips of the rays are set, resembling those of *L. timorense*.

Lissoclinum ravarava Monniot & Monniot, 1987 from French Polynesian and New Caledonia (Monniot, 1992) resembles *L. limosum*, but its zooids are only partially encapsulated in spicules, it has a large open cloacal cavity with the zooids crossing it in sheaths of test, instead of being embedded in the test, and it has only 2 pairs of ectodermal ampullae (Monniot, 1992).

Lissoclinum textrinum Monniot, 1992 from New Caledonia has yellow colonies, 6 larval lateral ampullae per side and the testis divided into 2. It otherwise resembles *L. caliginosum*, which is blue in life, has an undivided testis, some spicules more than 0.05mm diameter, and only 2 larval epidermal ampullae per side.

Lissoclinum tuheiavae Monniot & Monniot, 1987 and Monniot, 1992, from French Polynesia and New Caledonia has large (to 0.18mm between the tips of arms) sparsely distributed spicules with 4 or 5 long compacted arms and a central tuft of short needle-like rays (Monniot & Monniot, 1987, fig. 18i). The larval trunk is small (to 0.6mm long) with 4 pairs of lateral ampullae, and it lacks blastozooids. Monniot (1992) claimed that the spicules are like those of *L. taratara* and *L. philippinensis* Tokioka, 1967 (<*L. triangulum*) which are only about half the size of those of *L. tuheiavae* and have other differences. The spicules resemble those of *L. calycis*, but have a smaller central tuft of short needle-like rays. *L. pacificense* (Kott, 1981) has spicules that resemble those of the present species more closely, although they are only 0.064mm between the tips of the arms and it has a distinctive large larval trunk (to 1.2mm long), 6 round lateral ampullae on long narrow stalks each side of the 3 antero-median adhesive organs and 2 blastozooids per side. Monniot & Monniot (1987, pl. 4B,C) show scanning electron micrographs of spicules said to be from this species which do not resemble either their description or drawings (Monniot & Monniot, 1987, fig. 18i). These spicules, although they are the same size, have a solid central mass similar to *L. verrilli* from the Atlantic. The material from which these spicules were taken is not documented.

Lissoclinum tunicatum Monniot & Monniot, 1996 from the Coral Sea SE of New Guinea, resembles the *punctatum* group, having capsules of small (to 0.02mm diameter) regularly spherical burr-like spicules surrounding the zooids and embryos. It is difficult to assess the status of this species from the information given. Only one of its spicules has been figured (Monniot & Monniot, 1996, fig. 20c), and that resembles the spicules of *L. concavum*. *L. limosum* has a similar larva with about 20 epidermal ampullae surrounding the antero-median adhesive organs but it has a blastozooid which does not occur in the present species and it has more spicule rays.

Lissoclinum vareau Monniot & Monniot, 1987 from French Polynesia, is a mauve investing sheet, soft but crowded throughout with spicules. Zooids probably are suspended across the common cloacal cavity as in *L. reginum* — although the description is ambiguous. Like *L. reginum*, *L. vareau* has an atrial tongue and 2 male follicles, but it lacks a retractor muscle, and has twice the number of larval ampullae found in *L. reginum*. The scale indicated on the scanning electron micrograph of *L. vareau* spicules (Monniot & Monniot, 1987, pl. 4D) may be incorrect. The apparent size of the burr-shaped spicule is about 0.14mm diameter. However, the spicules are reported to be up to 0.04mm (Monniot & Monniot, 1987) — which seems more likely.

Lissoclinum verrilli (Van Name, 1902) is from the western, and possibly the eastern Atlantic (Millar, 1953). The species is characterised by its spicules and their distribution and by the firm colonies with zooids in long double rows, each zooid encapsulated in spicules. Despite the view that they are not (Monniot & Monniot, 1987), these characters are as reported by Van Name for the species. Further the larval tail is wound completely around the trunk. Spicules have a conspicuous compact central mass (Van Name (1902, 1945; Kott, 1982a). The spicules resemble, but are smaller than in *L. tuheiavae* (Monniot & Monniot, 1987, pl. 4B,C).

Lissoclinum vulgare Monniot, 1992 from New Caledonia is known only from a small white colony which like *L. taratara* has spicules throughout, a large common cloacal cavity, lacks a retractor muscle, has an entire testis follicle and a larval trunk 0.6mm long with 4 pairs of epidermal ampullae. It is distinguished from *L. taratara* only by its smaller spicules (to 0.04mm from tip to tip) and its smaller zooids.

Lissoclinum badium
Monniot & Monniot, 1996
(Figs 135, 176D; Pl.18C,D)

Lissoclinum badium Monniot & Monniot, 1996: 170.

NEW RECORDS. Western Australia (Bonaparte Archipelago, QM G302930). Queensland (Capricorn Group, QM G10158, G302075, G302105, G302979, G302986, G302988-91, G302994, G308078-80, G308081, G308200, G308273, G308324; Swain Reefs, QM G305707, G308384, G308393, G308395; Bowden Reef, QM G300941; Lizard I., QM GH5728).

PREVIOUSLY RECORDED. Western Pacific (Coral Sea, Palau Is – Monniot & Monniot, 1996).

COLONY. Colonies are very soft. In life they are stretched like a thin film over the surface of hard substrates, such as the under surface of rocks. When released from the substrate the colony

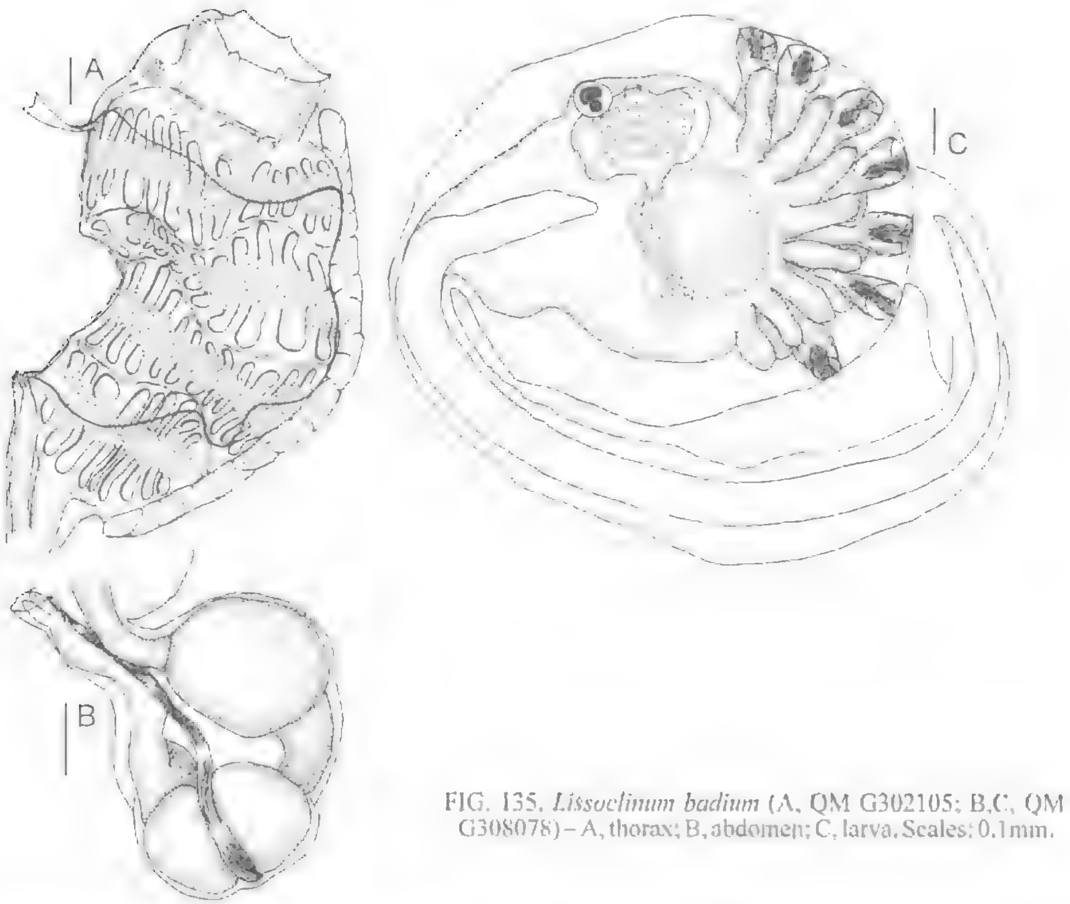


FIG. 135. *Lissoclinum badium* (A, QM G302105; B,C, QM G308078) – A, thorax; B, abdomen; C, larva. Scales: 0.1mm.

retracts into a thick rubbery looking spongy mass, with a yellowish-cream base and external margin. Living specimens are described as grey-green, dark grey, tiger coloured, or vandyke brown[R], or chocolate with patches of cinnamon[R], and with vandyke brown[R] or chocolate[R] coloured zooids and with some yellow in the surface test. The spherical brown and yellow pigment cells in the surface are either in separate patches or mixed. Large (to 5mm diameter) cloacal apertures, dark-brown inside, are on elevations maintained by pressure in the common cloacal cavity. The branchial apertures are seen as evenly distributed white points, the test around the apertures being crowded with spicules. Brown pigment is present throughout the surface layer of test and lines the common cloacal cavity. Both surface and basal test are thin, and a vast internal cavity is interrupted by the zooids in strands of test slung vertically across it. Thoraces are separate from one another. A number of abdomina are clumped together, or sometimes partially embedded in the basal test. Dark oval pigment cells (containing black granules) are in the test around the zooids, and in fairly evenly distributed spherical masses in the basal test.

Spicules are in the surface test mingled with the pigment, and are crowded around the branchial apertures. Sometimes they look like a dust of white over the surface. They become less crowded and sometimes are absent altogether from the strands of test around the zooids, but they usually are crowded in the basal layer of test. Sometimes they are missing from around the rims of the common cloacal apertures which are yellow, with an outer wide band of brown. Spicules are small (generally to 0.03mm in diameter although a few larger ones to about 0.04mm have been found) and burr-like, with many either rod- or needle-like rays.

In preservative, colonies are much the same colour as they were in life (brown and yellow). However, they never are the same shape. Thin, sheet-like films are never found in preservative, the colonies always being thick rubbery looking

irregular lumps. Living colonies of the same lumpy, rubbery appearance do occur if part of the colony has been dislodged from the substrate. The label of preserved specimens stains yellow brown. The yellowish-cream base and border results from the absence of pigment cells in those parts of the colony.

ZOOIDS. Zooids are fairly large, the thorax about 1mm, with 6 small branchial lobes. Atrial apertures expose the whole branchial sac to the common cloacal cavity. A pronounced tongue, usually bifid, projects from the upper rim of the opening. A round lateral organ is half-way down each side of the atrial opening. The anterior to posterior rows of stigmata have, respectively, 12,11,11,9 per row. In addition to the branchial sphincter, muscles are fine parietal ones and dorsal longitudinal pharyngeal bands fading out at the posterior end of the pharynx around the top of the ventral part of the oesophagus. A retractor muscle is not present. The gut loop has a long duodenum, a small oval posterior stomach, and the expanded proximal part of the rectum separated from the narrow cylindrical distal part by a conspicuous constriction. The 2 testis follicles have the straight vas deferens hooked around between them.

Embryos are incubated in the basal test. Large larvae were taken in March (QM G308078). The trunk is about 1mm long with the tail wound half-way around it, 8 lateral ampullae are along each side of the 5–9 antero-median adhesive organs. The oozooid is well developed with 4 rows of stigmata, but there is no blastozooid. Oval granular cells are crowded in the larval test as in other species of the *fragile* group.

REMARKS. The newly recorded specimens share most significant characters with the type material (Monniot & Monniot, 1996). However, the colonies are not thin, sheet-like and stretched over the substrate; only 10 stigmata are reported to be in the first row; the large brown pigment cells are said to have 'invaded' the body wall and branchial sac (Monniot & Monniot, 1996) and presumably are in the adult haemocoel; and the granular bodies have not been reported from the larval test.

The species is distinguished by its soft, inflated colonies, absence of a spicule-free superficial pigmented layer of test (present in *L. caliginosum*) its small spicules, yellow-brown pigment and brown cells in the test around the zooids and large larvae with more than 3 adhesive organs. A related species (with similar zooids, 10 lateral larval ampullae and burr-shaped spicules), *L. vareau* Monniot & Monniot, 1987, is mauve with only 3 larval adhesive organs, a smaller larval trunk, and spicules without as many and not such narrow rays. *L. japonicum* Tokioka, 1958 (see Monniot, 1992) has 6 lateral ampullae and 5 adhesive organs in the larva, but the zooids are smaller, and the atrial tongue is lacking.

L. fragile: Kott, 1976 (< *L. durabile*) from Western Port, has burr-like spicules to 0.03mm diameter, 2 male follicles, and a fairly shallow cloacal system but is distinguished by its brittle colony and shallow cloacal cavity.

Monniot & Monniot (1996) reported that the species has a strawberry odour.

Lissoclinum bistratum (Sluiter, 1905) (Figs 136, 178A; Pl. 18E–G)

Didemnum bistratum Sluiter, 1905a: 103; 1905b: 18; 1909: 46. Hartmeyer, 1909: 1449. Michaelsen, 1920: 48.
Lissoclinum bistratum: Kott, 1980: 16; 1981: 189; 1982a: 112; 1998: 87. Parry, 1987: 130.
Not *Lissoclinum bistratum* Monniot, 1994: 566 (< *L. timorense*).
Didemnum voeltzkowi Michaelsen, 1920: 54 (part, specimens ZMH K1111).
Lissoclinum voeltzkowi: Monniot, 1992: 579.
Didemnum gottschaldti Tokioka, 1950: 118.
Lissoclinum pulvinum Tokioka, 1954: 247; 1967: 97 (part).
Leptoclinum molle: Kott, 1962: 309; 1966: 289.
Lissoclinum molle: Tokioka, 1967: 95; Kott, 1977: 618.
Didemnum patella: Millar, 1963: 701.
Didemnum chartaceum: Kott, 1962: 324.

NEW RECORDS. Western Australia (Kimberley, WAM 790.91; Shark Bay, WAM 1052-3.83). Lord Howe I. (QM GH42). New South Wales (Hastings Point). Queensland (Heron I., QM GH5578, G301567, G301886, G301946, G301972; Swain Reefs, QM G305461, G308371, G308373-4; Big Broadhurst Reef, QM G300978; Hardy Reef, QM G308659; Flinders Reefs, QM G302161); Marion Reef (QM G10170).

PREVIOUSLY RECORDED. Queensland (Smiths Reef, Flinders Reef off Moreton Bay – Kott, 1982a; Mooloolabah, Mudjimbah – Kott, 1980; Heron I. –QM G9951 Kott, 1977; 1980; Green I. – Kott, 1980; Lizard I. – Kott, 1977). Northern Territory (Darwin – AM Y1341-2 Kott, 1966). Western Pacific (Coral Sea — Kott, 1980; Palau Is – Tokioka, 1950, USNM 11434 Tokioka, 1967, Kott, 1980; Caroline Is – Kott, 1982a; New Caledonia – Monniot, 1992; Philippines – Kott, 1982a); Fiji – Kott, 1980, 1982a). Singapore (Kott, 1982a). Indonesia (Sluiter, 1909). Japan (Tokara Is – Tokioka, 1967). Red Sea, Gulf of Aden (Sluiter, 1905a, b; ZMH K1107, K1108 Michaelsen, 1920). Malagasy (ZMH K1111, *D. voeltzkowi* Michaelsen, 1920, part).

The species is often found with *Trididemnum cyclops*, a species with a similar colony. It often occurs in crowded populations on sandy substrates on the open reef flat.

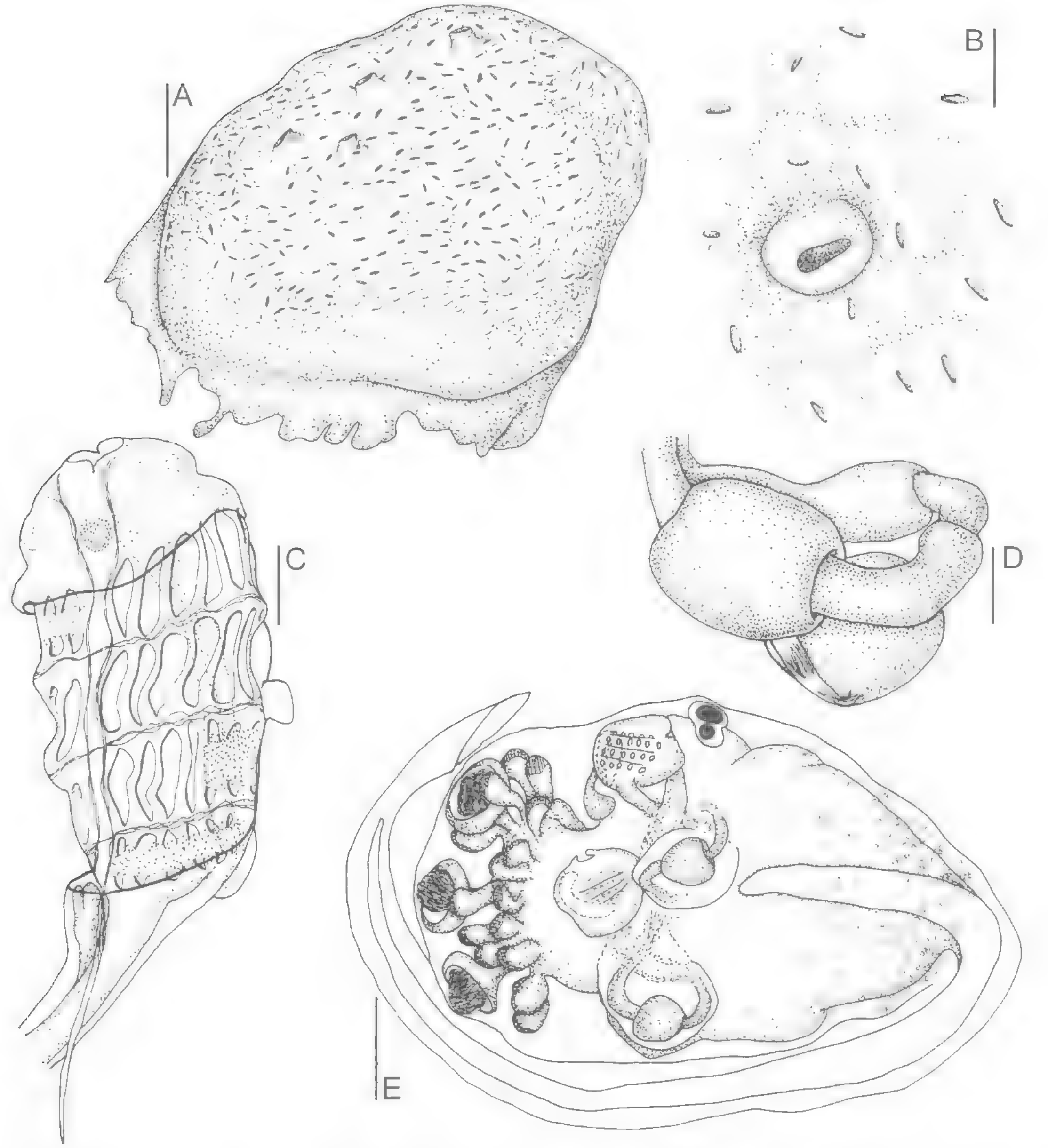


FIG. 136. *Lissoclinum bistratum* (A,B, QM G308373; C, QM G308374; D, AM Y1342; E, QM G9951) – A,B, external appearance showing protuberant common cloacal apertures and slit-like branchial apertures, whole colony and part of surface, respectively; C, thorax; D, abdomen; E, larva, showing *Prochloron* adhering to larval test around posterior end of trunk. Scales: A, 0.3mm; B, 0.5mm; C,D, 0.1mm; E, 0.2mm.

COLONY. Colonies usually are small, oval cushions to 2cm long, but sometimes are more extensive sheets to 5cm in maximum dimension. They are never more than about 5mm thick. One or more common cloacal apertures are on the upper surface. They are sessile or on short cylindrical chimnies sometimes bent horizontally — presumably in the direction of the prevailing current. Branchial apertures appear on the surface as small slits.

Common cloacal cavities are 3-dimensional, the thoracic spaces around the zooids connecting

with deeper spaces that surround groups of zooids. Spicules are crowded in the base and around the margins of the colony, although their concentrations in the surface test (over the cloacal chambers in which *Prochloron* symbionts are crowded) vary according to light falling on the colony (Parry, 1987) — few spicules are present when light intensity is reduced, for instance, on the under surface of rubble, rocks etc. Colonies in non-cryptic habitats e.g. on the upper reef flat, are protected by more crowded spicules, and a layer of carotenoid pigments in the thin superficial layer of test (Parry, 1987). Thus colonies vary from yellow or pink, to white to green as light intensity is reduced. Spicules always surround the branchial apertures and are drawn down into the siphons when they contract. Only a thin superficial layer of bladder cells is on the upper surface. Spicules are spherical to 0.05mm in diameter, with flat-ended cylindrical rays.

ZOOIDS. Zooids are up to 0.9mm long. The branchial aperture is a transverse slit, with a ventral and a dorsal lip. About 6 fine muscles radiate from each end of the slit and probably are homologues of the thoracic longitudinal muscles in other species that receive branches from the circular siphonal muscles. A narrow retractor muscle projects from the posterior end of the thorax. The atrial opening is wide, exposing the whole of the pharynx to the common cloacal cavity. A lateral organ is about halfway down each side of the thorax, everted into a flap projecting from each side of the atrial opening in some zooids after their removal from the test. The branchial sac has about 6 stigmata in each row. The gut loop is relatively short with a large rounded stomach but the post-pyloric part of the loop is short, and the duodenum and posterior stomach small. The proximal part of the rectum is wide, and it narrows opposite the stomach. A spherical undivided testis against the dorsal side of the distal part of the gut loop, has the vas deferens curved around its dorsal border.

Larvae are present in the basal test of colonies from Heron I. collected in December, January, March and October (Kott, 1980). The large trunk is about 1mm long, with the tail winding halfway around it. At least 8 pairs of ectodermal ampullae are along each side of the 3 antero-median adhesive organs. The tips of the epidermal ampullae have some columnar epithelium and may function as accessory adhesive organs. *Prochloron* cells adhere to the larval test only around the posterior third of the trunk. An oozooid and 2 blastozooids are in a vertical row about halfway along the trunk. A cerebral vesicle containing an ocellus and otolith protrude from the anterior end of the oozooid into the test.

REMARKS. The species is of particular interest in connection with its control of the light falling on its obligate *Prochloron* symbionts by variations in the concentration of carotenoids and spicules in the surface, and alterations in the ratio of chlorophyll a and b in the symbionts (Parry, 1987). *L. timorense* is a related species having stellate spicules with conical rays rather than spherical spicules. It lacks carotenoid pigments, and controls the illumination by the concentration of spicules in the surface test. Further, crowded populations of *L. bistratum* penetrate further south than *L. timorense* and may be more tolerant of diurnal temperature ranges in the reef top habitats of both these species.

Branchial apertures are similar transverse slits in *L. timorense* and *L. patella*. Monniot (1992) appears to have mistaken *L. timorense* for *L. bistratum* and vice versa. Both the larvae and the spicules of the specimens she assigned to *L. voeltzkowi* (<*L. timorense*) appear to be *L. bistratum*, and those assigned to *L. bistratum* are *L. timorense*, with fewer spicule rays and larger larvae than *L. bistratum* (Kott, 1980, pl. 1, fig. 3a). Monniot (1992) also referred to a rastrum in the larva — there is no rastrum in the larvae of *Lissoclinum* in which the *Prochloron* merely adhere to the test at the posterior end of the trunk. The immature larval trunk in the material assigned to *L.voeltzkowi* by Monniot (1992) is said to be spherical and enveloped in *Prochloron* cells. Neither one of these features have previously been recorded for either *L. bistratum* or *L. timorense*, although the symbionts on the larvae of *Trididemnum cyclops*, *T. miniatum*, *T. strigosum* and *T. clinides* do completely envelope the trunk.

As well as the smooth colony surface, globular spicules, carotenoid pigment, and slit-like branchial apertures, conspicuous characteristics of the present species are its short gut loop and the presence of a retractor muscle.

Lissoclinum caliginosum sp. nov.
(Figs 137A,B, 177C)

TYPE LOCALITY. Queensland (Heron Is., eastern end of reef, below low tide, coll. P.Kott 09.03.93, holotype QM G308082, paratypes QM G308083).

FURTHER RECORDS. Queensland (Capricorn Group, QM G302983, G308089, G308271).

COLONY. Colonies are soft irregular mats. The superficial layer of test usually is free of spicules, and even in preservative is crowded with dark, sometimes black, spherical pigment cells, which also surround the zooids. The pigment is confined to the upper layer of test and is not in the base. Occasionally patches of spicules also are in the superficial layer of test. Spicules invariably are present beneath the superficial pigment layer, as well as in the test sheaths around the zooids, and they always are crowded in the basal layer of test. The spicules are up to 0.09mm, with numerous needle-like rays and a few have rod-like, flat-tipped rays. In life the colony is drab or dark and coloured dragons blood[R] or prune purple[R]. Zooids are orange in living and freshly preserved specimens.

Common cloacal cavities are large, zooids being slung vertically across these spaces in their spicule-containing strands of test. Several abdomina are clumped together but thoraces are separate from one another. Common cloacal apertures are large. In preserved specimens their rims are frilled because the whole colony retracts when it is removed from the substrate.

ZOOIDS. Zooids are large, nearly 2mm long, the thorax about equal to the abdomen. Six fine branchial lobes surround the aperture. Neither retractor muscle nor atrial lip are present. A large vertical flap-like lateral organ projects from half-way down each side of the atrial aperture, which is withdrawn back to the endostyle, exposing the branchial sac directly to the cloacal cavity. Twelve long stigmata are in the anterior row, 11 in the middle rows and 10 in the posterior row. The oesophageal neck is moderately long. The gut loop is rounded, looping ventrally over a large undivided testis with a straight vas deferens.

Embryos are being incubated in the thin basal test in specimens collected in March (QM G308082-3) and September (QM G308271). The larval trunk is about 0.6mm long, and almost spherical. The tail is wound halfway around it. Larvae are encased in a layer of opaque granular bodies embedded in the larval test as in other species of the *fragile* group. These are absent over the cerebral vesicle (with the ocellus and otolith) and over the anterior end of the 3 or 4 large, deep, antero-median adhesive organs. Two small, finger-like lateral ampullae are on each side of the adhesive organs. Blastozooids were not detected.

REMARKS. Diagnostic characters for the present species include the thick pigmented superficial spicule-free layer of test, its unusual larvae with deep adhesive organs and only 2 pairs of lateral ampullae, and the zooids which lack an atrial tongue and retractor muscle and have an undivided testis. The soft, dark colonies retract into thick mats when they are removed from the substrate, and resemble colonies of *L. badium* to some extent. However, they are never as extensive as the colonies of *L. badium*, and they never form such thick, rubbery masses. Also, the spicules of the present species are larger and the spicule rays are more numerous and thinner than those of either *L. badium* or *L. reginum*. A retractor muscle is present in the latter species, and both have an atrial tongue and a divided testis, and smaller spicules than the present species.

Like the present species, *L. conchylium* lacks a retractor muscle and an atrial tongue, but is distinguished by its 2 male follicles and smaller spicules. *L. vareau* Monniot & Monniot, 1987 from French Polynesia and New Caledonia also lacks a retractor muscle and has similar but probably smaller spicules, a different larva with numerous lateral ampullae, and a more delicate colony.

Lissoclinum calycis Monniot, 1992
(Figs 137C,D, 177B)

Lissoclinum calycis Monniot, 1992: 568.

NEW RECORDS. Queensland (Heron I., QM G308339).

PREVIOUSLY RECORDED. New Caledonia (Monniot, 1992).

COLONY. In life the colony is an extensive, encrusting, thin sheath with white-yellow zooids. Thoraces are white and translucent, while the abdomina have brownish-yellow stomachs showing through a capsule of white spicules. The test is very soft and in preservative is transparent and mucus-like, and the zooids, with the abdomina encapsulated in white tetrahedral spicules, are conspicuous. The spicules have 4 pointed arms, each consisting of several long thick rays crowded together. The central part of each spicule has thin needle-like rays of varying size becoming longer out along the base of each of the 4 arms. The larger spicules measure to 0.125mm between the pointed tips of 2 of the arms.

ZOOIDS. Zooids are small (0.8mm long), transparent, without a retractor muscle. The thorax is very much contracted, the abdomen

bent up at right angles to the long axis of the zooid, and a large testis is posterior to the loop, against its dorsal surface. The atrial aperture is large, without an atrial tongue. The gut is divided into stomach, long duodenum, long posterior stomach and rectum. The testis is undivided and the straight vas deferens is hooked around its posterior margin. The ovary, with one large egg

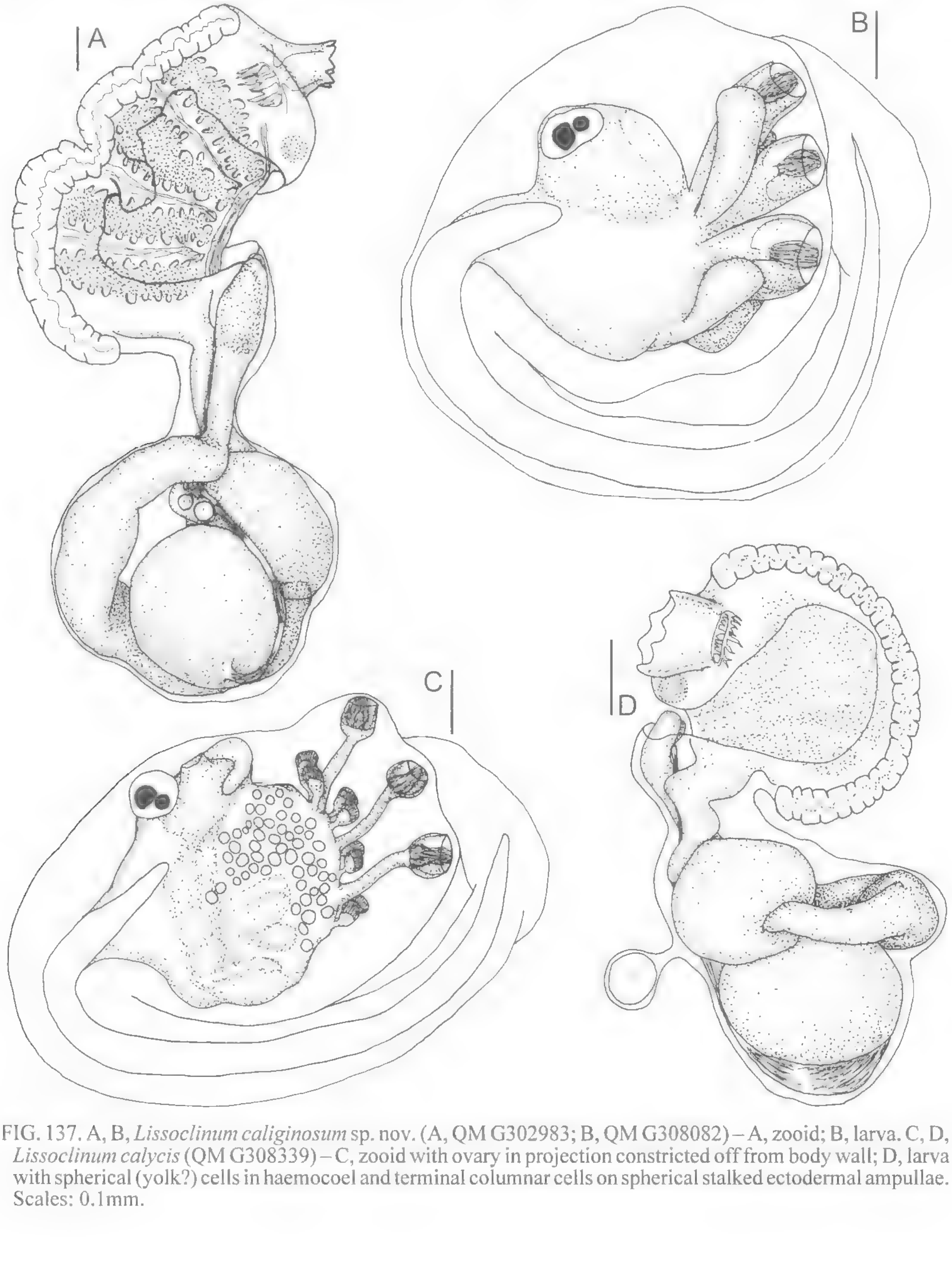


FIG. 137. A, B, *Lissoclinum caliginosum* sp. nov. (A, QM G302983; B, QM G308082) – A, zooid; B, larva. C, D, *Lissoclinum calycis* (QM G308339) – C, zooid with ovary in projection constricted off from body wall; D, larva with spherical (yolk?) cells in haemocoel and terminal columnar cells on spherical stalked ectodermal ampullae. Scales: 0.1mm.

and 3 or 4 small undeveloped ones projects out from the abdomen from a point just in front of the testis. The developing egg is constricted off entirely from the body wall of the zooids.

Many embryos are present in the soft test of the newly recorded material (collected in September). The fully developed larva has a trunk 0.7mm long with the tail wound only half-way around it. The larva contains a rich supply of large yolk cells in the anterior part of the trunk. Posteriorly 2 blastozooids develop, seemingly by strobilation of the abdomen of the oozooid. The branchial sac of the oozooid is shallow and compressed at the top of the trunk, and the cerebral vesicle protrudes from the upper surface. Three antero-median adhesive organs are thistle-shaped, on slender stalks with a deep adhesive cone on a narrow base. Four lateral ampullae are along each side of the adhesive organs. The ampullae have almost spherical tips, consisting of a rounded cap of columnar cells and are on narrow stalks.

REMARKS. The species is characterised by its soft colonies with spicules encapsulating the zooids, size and form of spicules, zooids with the gut at right angles to their long axis, large male follicle and size and form of the larvae, with 4 narrow-stalked lateral ampullae per side, protuberant cerebral vesicle, shallow larval thorax, large yolk mass and 2 blastozooids apparently developing from the gut loop of the oozooid at the posterior end of the trunk.

In outline the spicules resemble the tetrahedral spicules in other species of this genus. However, they are distinguished by the fine needle-like rays separate from one another in the central mass of the spicule. Other species, such as *L. tasmanense* (Kott, 1954), and *L. verrilli*: Monniot & Monniot, 1987 with spicules encapsulating the zooids, have compact tetrahedral spicule rays with or without a large, compact central mass. *L. triangulum* has needle-like spicule rays, sometimes forming points in the outline of the spicule. However, these are more or less flattened, unlike the spicules of the present species. The spicules resemble those of *L. tuheiavae* Monniot & Monniot, 1987 and *L. pacificense*, although both have a smaller central mass of needle-like rays, and although the former species has spicules the same size as *L. calycis*, the latter has spicules less than half the size. The larva has blastozooids like *L. pacificense* but has only 4 pairs of ectodermal ampullae and is the same size as *L. tuheiavae*.

Lissoclinum concavum sp. nov.
(Figs 138A–C, 178G; Pl. 18H)

TYPE LOCALITY. South Australia (Franklin I. just E of almost exposed reef about 1km N of sandbar between islands with large rock outcrops 13-5m, coll. W. Zeidler, P. Aerfeldt et al., 22.2.83, holotype SAM E2691).

FURTHER RECORDS. South Australia (Flinders I., QM G308447 – specimen lost, slide only; Wright I., SAM E2666).

COLONY. The holotype colony is extensive, encasing a weed stalk. The basal test is of variable thickness reaching 6 to 7mm in some places. In the preserved colony, brown zooids suspended in the cloacal cavity, together with the soft, thick surface layer of test, form an even, brown layer about 3mm thick. The brown colour shows through the layer of spicules in the test strands that encase the zooids either separately or in clumps of 2 or 3. Zooids are grouped into separate systems to 5mm in diameter around a central common cloacal aperture. Common cloacal cavities are isolated from one another by white spicule-filled vertical walls of test between the surface and basal test. Common cloacal apertures are conspicuous and sessile, surrounded by branchial apertures which are neatly depressed into the otherwise smooth, even surface. Each stellate branchial aperture has a margin of white spicules which line the siphon, but each aperture is surrounded by a circle of spicule-free test in the base of each depression, partly overlaid around the periphery of the depressed area by the even rim of the surface test containing evenly distributed, although not crowded, spicules. Spicules are variable in their distribution, sometimes being less crowded in the basal layer of test, although in a colony from Flinders I. the spicules are sparse, forming clouds in both surface and basal layers of test. Small, immature (without gonads), specimens from Wright I. (SAM E2666) have spicules evenly distributed throughout the soft and slightly translucent colonies growing along a flat seagrass blade.

Spicules are mostly small (to 0.035mm in diameter) although occasionally some reach 0.06mm diameter. They are mostly burr-shaped, although a few are stellate, the burr-shaped ones with rather loose rays each made up of crowded needles. The rays, up to 15 in optical transverse section, often are tongue-shaped but others are pointed, uneven, or with flat or rounded tips. Numerous morula bodies also are in the test, making it cloudy.

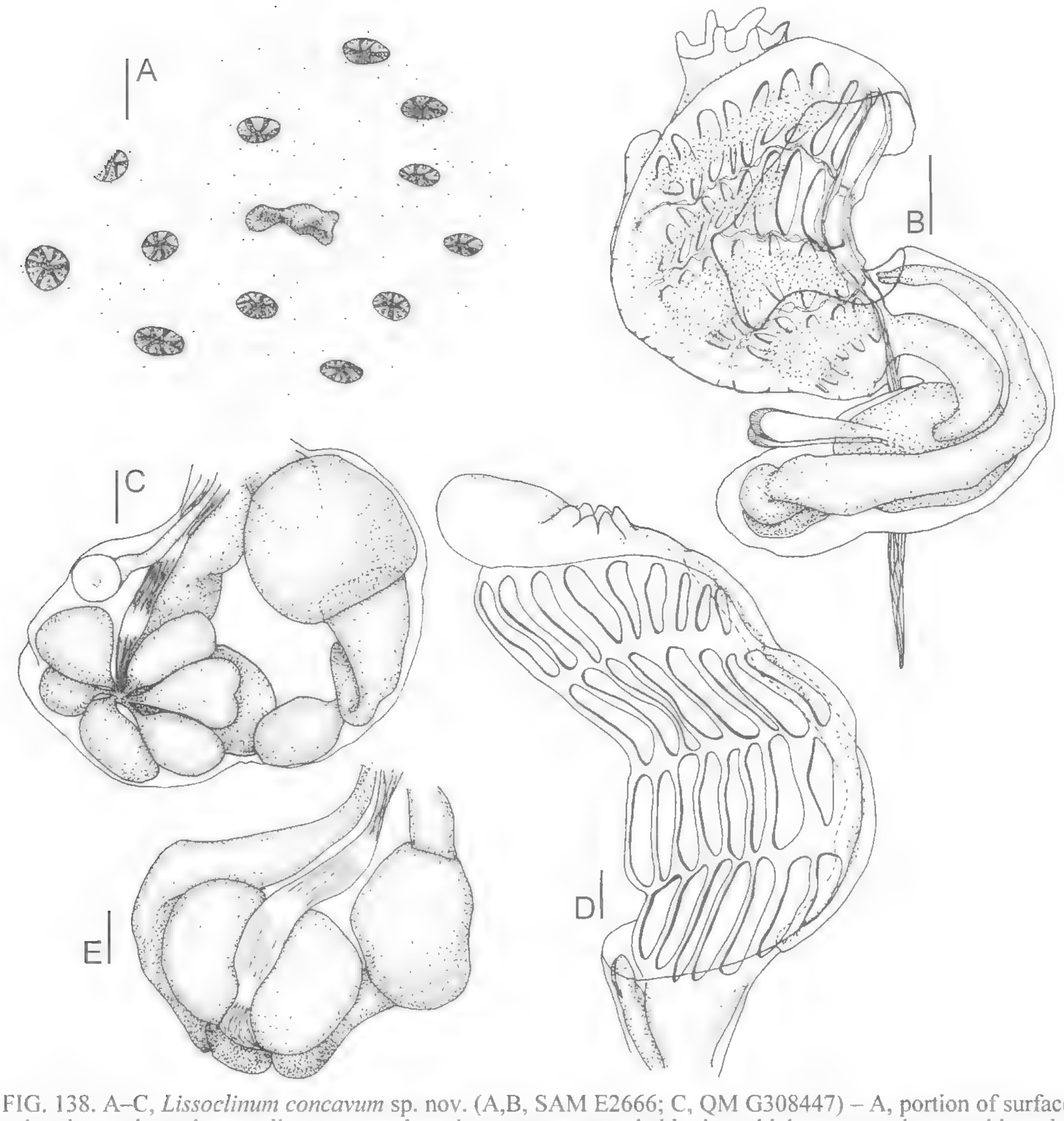


FIG. 138. A–C, *Lissoclinum concavum* sp. nov. (A,B, SAM E2666; C, QM G308447) – A, portion of surface showing an irregular, sessile common cloacal aperture surrounded by branchial apertures depressed into the surface; B, zooid; C, gut and gonads. D, E, *Lissoclinum conchylium* sp. nov. (QM G308321) – D, thorax; E, abdomen. Scales: A, 0.5mm; B–E, 0.1mm.

Large isopods are in the cloacal cavity of the holotype.

ZOOIDS. Zooids are relatively large, in mature colonies to about 1.5mm long, although many in juvenile specimens (SAM E2666) are smaller. The relaxed thorax is larger than the abdomen which is bent up ventrally alongside the posterior end of the right side of the thorax. Even a contracted zooid with the abdomen in its flexed position is about 1.5mm long. The branchial aperture is short, and has 6 pointed to narrow finger-like lobes around its rim. The atrial aperture is a large opening which, in expanded zooids, exposes most of the branchial sac to the cloacal cavity. A retractor muscle of variable length, often inconspicuous, projects from the upper part of the oesophagus. A large lateral organ is on each side of the thorax. In the branchial sac, 9 long rectangular stigmata are in the anterior row and 6 are in the posterior row. The oesophageal neck is of moderate length. The

proximal part of the oesophagus is vertical but the distal third bends ventrally at right angles to the vertical. The stomach is relatively small, a long duodenum leads to a small posterior stomach in the pole of the almost horizontal gut loop, although the proximal limb of the loop is higher (often to the right of the posterior end of the thorax) than the distal limb. A conspicuous constriction, with tubules of the gastro-intestinal glands around it is near the proximal end of the rectum. Vascular appendages project from the abdomen on the ventral (concave) side of the gut loop. A short, fine retractor muscle projects from the posterior end of the thorax.

The testis is posterior and dorsal to the ventrally flexed gut loop. It is divided into 6 pyriform follicles arranged in a circle with their narrow ends converging into the centre where they join the straight vas deferens. Larvae are not known.

REMARKS. Two species of *Lissoclinum* with numerous testis follicles are now known from Australian waters. In addition to the present temperate species, *L. multifidum* (Sluiter, 1909), which differs in the absence of spicules, is known from the tropics.

Monniot (1992) recorded *L. cornutum* and *L. polyorchis* from New Caledonia with a number of testis follicles. Both have different and generally larger spicules. In the former they are distinctly stellate, while in the latter they are like *L. timorense*. Also, in *L. polyorchis* the spicules are crowded around the margins of the colonies, and are less diverse. *L. variabile* has a similar colony and a similar diversity of spicules although its testis is only divided into 2. Spicules are most like those of *P. pontoniae* although there are generic differences between the species.

The appearance of the colony, with its branchial apertures depressed into the surface, is similar to other species in this genus (e.g. *L. conchylium*, *L. durabile*). The present species differs in the form of its spicules, the form of its cloacal systems, its soft colonies and its numerous testis follicles.

Lissoclinum conchylium sp. nov.
(Figs 138D,E, 176F; Pl. 19A)

TYPE LOCALITY. Queensland (Heron I., eastern end of reef, below low tide, coll. P.Kott 04.09.94, holotype QM G308321).

FURTHER RECORDS. Queensland (Moreton Bay, QM G308499).

COLONY. The colony is a fairly extensive, thin, investing sheet. Spicules, crowded throughout, make it hard, rigid and brittle. In life it is plum[R]- or pansy-purple[R], the pigment persisting in preservative, so that the colony remains a pinkish-mauve colour. The purple pigment is in the surface, mixed with surface spicules. There is no spicule-free bladder cell layer. In preservative the thin surface test, crowded with spicules, is wrinkled owing to contraction after the colony was removed from the substrate. Some minute spicule-filled papillae are on the surface. Branchial apertures are evenly distributed, about 1.2mm apart, and slightly depressed into the surface. When open they appear smooth-rimmed and circular, surrounded by spicule-filled hard test, although they look stellate when partially closed. Common cloacal apertures are few, sessile, large and circular, up to about 5mm diameter. The common cloacal cavity is extensive with clumps of abdomina (partially embedded in the basal test) protruding up into it. The basal test is relatively thick and hard. The thoraces are separate from one another, crossing the cloacal cavity each in a separate ventral test strand crowded with spicules. In preservative zooids have brown pigment cells around the thorax, but not the abdomen. Brown cells are in the haemocoel.

Spicules are globular and burr-like, up to 0.055mm in diameter, with numerous long rod-shaped rays.

ZOOIDS. Zooids are relatively large, about 2.0mm long, the thorax slightly longer than the abdomen. The rim of the atrial aperture is drawn right back to the endostyle exposing the whole branchial sac to the cloacal cavity. An atrial lip is not present, nor is there a retractor muscle. Nine stigmata are in the 3 anterior rows of the branchial sac, and the posterior row has 7.

The gut loop is simple and rounded, flexed ventrally over the two male follicles. The vas deferens hooks around between them. Larvae are not available in either of the known colonies.

REMARKS. The hard, brittle colony is similar to *L. fragile*: Monniot, 1992, however, spicules are larger, and the persistent and distinctive colour distinguishes it. Blue, purple or rose-mauve colonies from the western Pacific are: *L. reginum*, with spicules mixed with pigment in the superficial test, is not hard and brittle like the present species, and it has a retractor muscle and atrial tongue; *L. caliginosum* has an undivided testis and larger spicules with more pointed rays;

L. vareau Monniot & Monniot, 1987 (Monniot, 1992) lacks a retractor muscle but has an atrial tongue and is softer, without the crowded spicules and hard colony; and *L. japonicum* Tokioka, 1958, has spicules to 0.03mm diameter crowded throughout. *L. japonicum* has only the size of its spicules distinguishing it from the present species, although its larvae (with 5 adhesive organs and 6 lateral ampullae) may eventually provide a further distinction (when the larva of *L. conchylium* is known). Temperate *L. durabile* has much in common with the present species, having crowded globular and burr-shaped spicules to 0.05mm with 15 or more rays, 2 testis follicles, and abdomina embedded, or partially embedded, in the base of the colony. The present species is distinguished by its large, sessile common cloacal apertures.

Lissoclinum durabile sp. nov.
(Figs 139A–C, 176H; Pl. 19B)

Lissoclinum fragile: Kott, 1976: 70.

TYPE LOCALITY. South Australia (West I., boulder slope, under boulder 5m, coll. S.A. Shepherd 27.11.66, holotype SAM E2663; Wright I. exposed side 10m, coll. S.A. Shepherd 28.11.66, paratype SAM E2667).

FURTHER RECORDS. Western Australia (Esperance, SAM E2848). Victoria (Western Port – Kott, 1976). New South Wales (Coffs Harbour, MV F70229).

COLONY. Colonies are hard, rigid and flat sheets with a smooth surface. Branchial apertures, in spicule-free thin surface test, are depressed into the surface of these preserved colonies and are surrounded by the rigid circular, hard edge of the spicule-filled surface test. Spicules are not in the siphonal linings. Crowded minute spicule-filled papillae sometimes are present on the surface. Spicules are otherwise packed throughout the colony. They are burr-like, to 0.04mm diameter, with 15 or more flat-tipped to club-shaped rays in optical transverse section. The cloacal cavity is thoracic, thoraces crossing it with their ventral surface either embedded in firm vertical stands of solid test, or separate from one another with an independent ventral strand of spicule-filled test. A vertical flap-like projection of spicule-filled test from the lateral organ is on the edge of the ventral test sheath on each side of the thorax. Abdomina are partially or completely embedded in the thick basal layer of test. Thoraces are brown in the preserved material with brown spherical (blood?) cells in the haemocoel. The brown colour is clearly seen through the circular spicule-free areas in the surface. Common cloacal apertures on short, protuberant cylindrical elevations about 1cm apart may be permanently open. Living specimens are yellow around the zooids and there is some reddish test between them (SAM E2848)

ZOOIDS. The delicate zooids are firmly held by hard, spicule-filled test, and are difficult to remove. Thoraces are long and are not contracted, adhering closely to the test in the preserved material with their long, rectangular stigmata stretched out. Branchial siphons are short with 6 short, rounded lobes surrounding the apertures and a mass of spherical yellowish green (possibly blood) cells in the siphon wall. The atrial aperture is very large, sessile. A short, narrow atrial tongue adheres closely to the test and is obscured by spicules or is torn if attempts are made to remove the zooid from the test. An almost spherical lateral organ which sometimes is everted (MV F70229) is on each side of the thorax between the second and third rows of stigmata on each side of the endostyle — the parietal thoracic wall being withdrawn to expose the whole of the branchial sac to the cloacal cavity. A fine, short retractor muscle is present but difficult to demonstrate. A few fine muscle fibres are in each transverse vessel between the rows of stigmata and a delicate longitudinal pharyngeal muscle is each side of the mid-dorsal line. About 8 stigmata per row are in the branchial sac. The gut loop is rounded, bent up at right angles to the thorax. It has the usual divisions. The vas deferens curves around between the 2 testis follicles against the ventrally flexed gut-loop at the posterior end of the body before extending anteriorly with the rectum. Larvae are not known.

REMARKS. Like some other members of the *fragile* group, the species has brown cells in the haemocoel. The thoracic cloacal cavity and the form and distribution of spicules closely resemble *L. conchylium* from which the species is distinguished by its regularly distributed, elevated, circular common cloacal apertures, thicker basal test and colour. The species is distinguished from the sympatric *L. ostrearium* (which also has 2 testis follicles and lacks a retractor muscle) by its more restricted cloacal cavity and larger spicules. The thoracic cloacal cavity also distinguishes it from certain tropical species, in particular *L. reginum* and *L. badium* which have similar spicule-free areas around the branchial openings interrupting the otherwise crowded burr-like spicules. Although a similar size, spicules of both tropical species have more numerous and finer spicule rays. The depressed

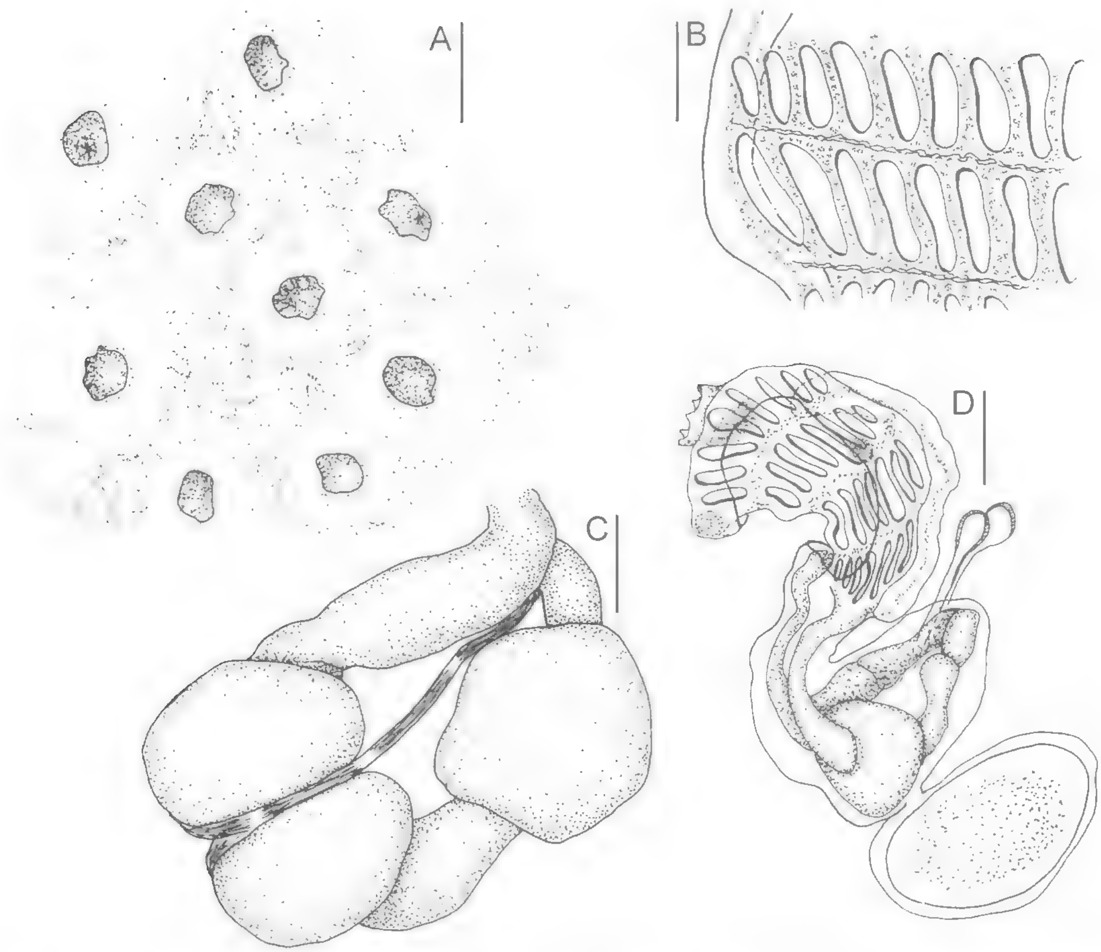


FIG. 139. A–C, *Lissoclinum durabile* sp. nov. (A,C, SAM E2663; B, SAM E2848) – A, part of colony surface showing depressed branchial apertures; B, portion of branchial sac showing brown cells in the haemocoel; C, abdomen. D, *Lissoclinum levitum* sp. nov. (QM GH2420) – D, zooid. Scales: A, 0.5mm; B–D, 0.1mm.

branchial apertures also occur in other *Lissoclinum* spp. (e.g. sympatric *L. concavum*)

Kott (1976) assigned Western Port specimens of the present species to *L. fragile*, together with suggested synonyms (from tropical and temperate waters of the Pacific and Atlantic oceans). Although they all share generic characters, Kott was incorrect in regarding them as conspecific. The more restricted thoracic cloacal cavity of the present species distinguishes it.

Lissoclinum levitum sp. nov.
(Figs 139D, 176-I; Pl.19C)

TYPE LOCALITY. South Australia (Ward I., Investigator Group, in caves 8m, coll. N. Holmes 12.4.83, QM GH2420).

COLONY. The colony is a flat, thin sheet. Dark zooids show through the not very crowded but evenly distributed spicules to affect the colour of the preserved specimen. Spicules are moderately crowded in the surface layer of test and in the base of the colony, but are relatively sparse in the middle (at zooid level), so that the centre of the colony is brown, owing to the pigment in the zooids, and is sandwiched between white surface and basal layers of test. A few large, fleshy common cloacal apertures around the margin of the colony look whiter than the remainder of the surface owing to the absence of zooids and slightly more crowded spicules than in the remainder of the surface test. Spicules are in the surface test, and a spicule-free layer of bladder cells does not occur. Spicules are of variable size, occasionally being up to 0.035mm in diameter

but most being smaller, seldom more than 0.02mm diameter. They have 11–13 long, almost fusiform rays in optical transverse section. Ray length/spicule diameter ratio is about 0.38. Restricted common cloacal canals are at thorax level, with zooids along each side of them with the branchial sacs exposed directly to the cavity through the large atrial apertures. The abdomina and the postero-ventral parts of the thoraces are embedded firmly in the basal test.

ZOOIDS. Zooids are difficult to remove from the test, and were examined in hand cut decalcified sections. Thoraces are long and narrow, with short branchial siphons and shallow branchial lobes. The atrial aperture exposes the whole of the branchial sac to the common cloacal cavity. Eight long stigmata are in the 2 anterior rows and 7 in each of the posterior rows. A lateral organ is about halfway down each side of the thorax, on the edge of the atrial aperture. A retractor muscle was not detected. The abdomen is bent up ventrally and to the right of the posterior end of the thorax. The oesophagus is long, and curves ventrally and to the right, the stomach, duodenum and posterior stomach are almost at right angles to the long axis of the thorax. Testes are not present in the holotype colony, but a large early embryo projects posteriorly in a brood pouch constricted off from the abdomen by a narrow neck. Two relatively short vascular appendages project from the ventral concavity of the flexed gut loop. The larva is not known.

REMARKS. Despite the absence of male gonads, it is possible to assign this specimen to *Lissoclinum* on the basis of the long, narrow thorax with long stigmata, a large open atrial aperture, a short branchial siphon, the position of the abdomen (bent up to the right of the posterior end of the thorax), and the large egg in a brood pouch attached to the zooid by a constricted neck. The species resembles *L. durabile* (from southern Australia) in its spicules and its restricted cloacal canals. However, *L. durabile* colonies are hard, with spicules crowded throughout and these have rays with flatter and more rounded tips; and its zooids have a retractor muscle. The spicules are like those of *L. ostrearium*, although they have fewer rays. Spicules of *L. concavum* are of similar size, with similar numbers of rays, but the rays are flat-tipped.

Lissoclinum limosum sp. nov.
(Figs 140A,B, 177F; Pl. 19D)

TYPE LOCALITY. Queensland (Heron I., north reef – Cascades, low tide rubble fauna, coll. P. Kott 2.5.85, holotype QM G301746, paratypes QM G308357; N.W. Wistari Reef, low tide rubble fauna, coll. P. Kott 11.11.85, paratype QM G302325).

FURTHER RECORDS. Queensland (Capricorn Group, QM G302310, G302319, G302323, G302330, G302998; Swain Reefs, QM G308419).

COLONY. Colonies are small, thin and soft cushions up to 2cm in maximum extent with rounded margins. They disintegrate readily when removed from the substrate. In life the test is translucent, with black pigment surrounding each zooid, outside the single layer of spicules which completely encapsulate the abdomina and the developing embryos (in the basal test) and partially encapsulate the thoraces. The living colonies are said to resemble a *Botryllus* colony with the white encapsulated zooids appearing petal-like surrounded by black pigment. In preservative the whole test is brownish black and opaque, almost completely concealing the white capsule of spicules around each zooid. Zooids are embedded in the test, their atrial apertures opening directly into the relatively restricted thoracic cloacal cavities. When zooids are removed from the test in their capsules of spicules a layer of the very soft test clings to them and is not readily removed.

Spicules are confined to the capsules surrounding the zooids and embryos. They are not more than 0.03mm in diameter, with many radially arranged needle-like rays of slightly different lengths. Spicules are in the strip of test down the ventral part of the thorax forming a partial capsule that exposes the dorsal surface.

ZOOIDS. Zooids are small, less than 1mm long, with the distal part of the gut loop at right angles to the longitudinal axis of the body. The branchial siphon is short, with 6 pointed lobes around the rim of the aperture. No retractor muscle was detected. The atrial aperture is a large opening. The testis is undivided.

Embryos are developing in the basal test of colonies taken in November from the Capricorn Group (QM G302325). Although many are present, only a few are sufficiently advanced to determine the structure of the larvae. The larval trunk is 1.0mm long, almost spherical, with 3 median adhesive organs with deep ectodermal cups and axillary cones. An oozooid and a single blastozooid are in the posterior half of the trunk and 10 ectodermal ampullae are along each side

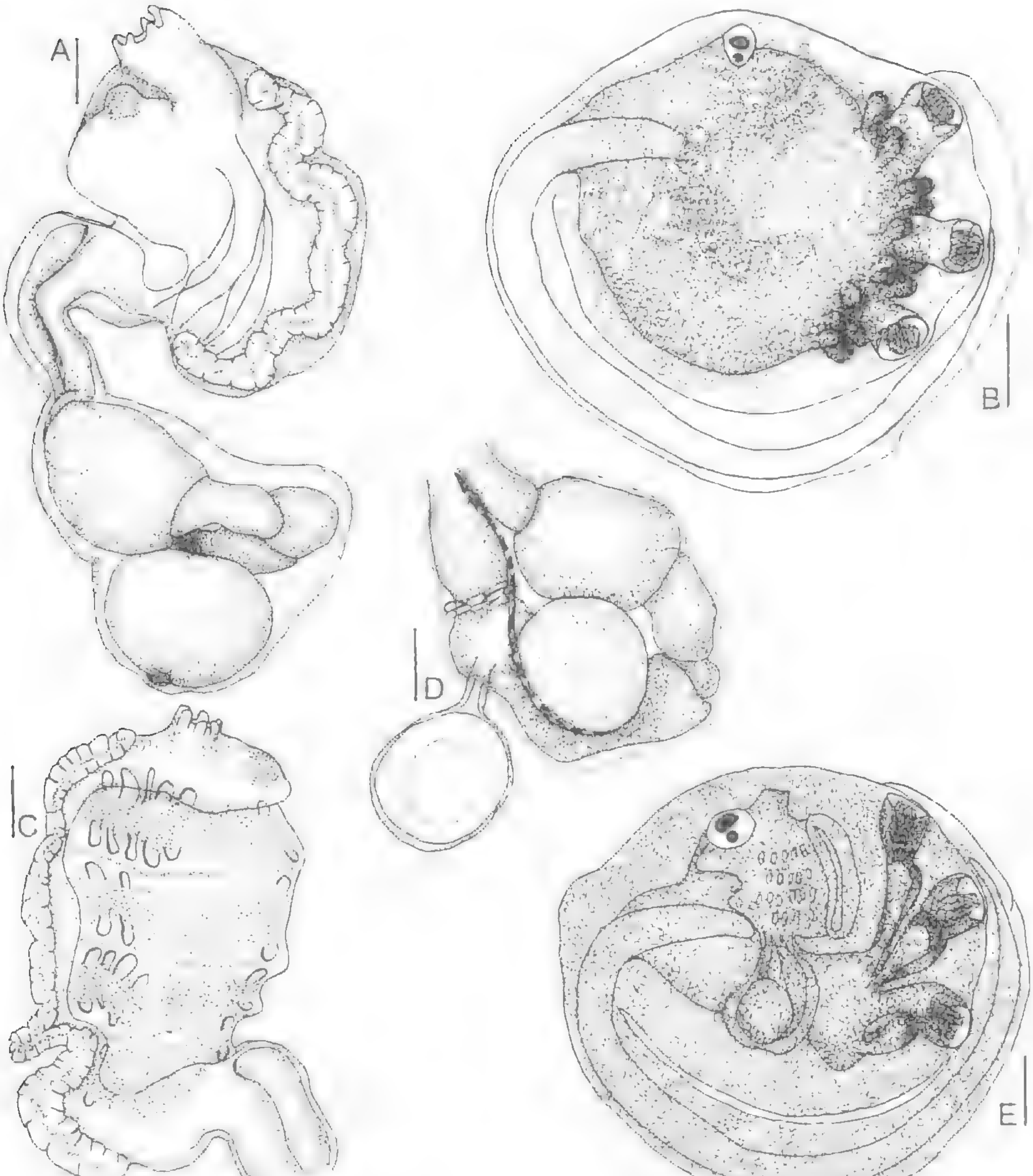


FIG. 140. A, B, *Lissoclinum limosum* sp. nov. (QM G302325) – A, zooid; showing individed testis B, larva showing opaque cells in the larval test obscuring oozooid and blastozooid, and the short rounded ectodermal ampullae with terminal columnar cells. C–E, *Lissoclinum maculatum* sp. nov. (QM G302236) – C, thorax contracted; D, abdomen showing tubules of gastro-intestinal gland around gut, and egg projecting in a brood pouch constricted off from the body wall. E, larva with opaque cells embedded in larval test absent only from circular areas over the cerebral vesicle and in front of each adhesive organ and terminal columnar cells on the tip of each ectodermal ampulla. Scales: A,C–E, 0.1mm; B, 0.2mm.

of the 3 antero-median adhesive organs. The tail is wound about two-thirds of the distance around the trunk. The larval test contains pigment cells, mixed with opaque cells, especially crowded around the posterior end of the trunk.

REMARKS. The species most closely resembles *L. tunicatum* Monniot & Monniot, 1996, apparently differing only in its lesser number of thicker spicule rays. It also resembles *L. ravarava* Monniot & Monniot, 1987 from French Polynesia and New Caledonia (Monniot, 1992) in its soft test and small burr-like spicules at least partially encapsulating the abdomina, although *L. ravarava* has only 2 ectodermal ampullae per side (Monniot, 1992). *L. roseum* has similar spicules and a similarly soft mucus-like test, but it lacks the dark pigment.

The larva of the present species resembles that of *L. tasmanense* which has a similar number of ectodermal ampullae. However, these species are not alike in any other way. *Lissoclinum mereti* Monniot & Monniot, 1987 and *L. triangulum* have flattened and very much larger and less regular spicules encapsulating the zooids.

In life, the present species is readily distinguished by its transparent test and dark pigment around the white capsules of the zooids. In preservative the soft black test and encapsulated zooids are distinctive. The zooids are smaller than those of *Diplosoma listerianum*, which also lacks the capsules of spicules around the zooids and has a characteristic pattern of black squamous epithelium in the body wall.

Lissoclinum maculatum sp. nov.
(Figs 140C–E, 177D)

TYPE LOCATION: Queensland (Lizard I., north reef, low tide rubble fauna, coll. P. Kott et al., 5.6.80, syntypes QM G302236).

COLONY. Colonies are small cushions 0.2–1.0cm in maximum dimension. Spicules are crowded around the outer margins and in the base of the colony, but are less crowded over the upper surface and throughout the remainder of the test. They are small, to 0.02mm in diameter, and burr-shaped, with numerous crowded rays with rather uneven, frayed tips. In the preserved colony, reddish brown pigment cells are in the superficial layer of test, generally mixed with spicules. Over the zooids the reddish brown colour is emphasised by the absence of spicules. Up to 3 small common cloacal apertures are evenly spaced in the centre of the larger colonies. Large, brown, spherical vesicles about 0.1mm in diameter are in randomly distributed patches in the surface. Root-like processes grow out from the margins of the colonies fixing them to the substrate. In life the colonies are salmon-pink[R] to rose[R], with vinaceus rufus[R] zooids and patches of dahlia purple pigment cells scattered through the translucent test.

The common cloacal cavity is vast, occupying most of the thickness of the colony, and the entire length of each zooid is suspended vertically in it by individual strands of test connecting the thin surface and basal layers.

ZOOIDS. Zooids have a relatively large thorax, always contracted, the branchial siphon is short and the rim of the aperture has 6 small lobes. Neither atrial lip nor retractor muscle were detected. The testis follicle is undivided.

Embryos are developing in brood pouches in the test strands, where they remain attached to the abdomen of the parent zooid until, at a late stage of development, they appear in the surface test. Sometimes the tail is being withdrawn into the larval trunk before the larvae are released, presumably through the surface. The larval trunk is 0.6mm long and almost spherical. The oozooid is halfway along the trunk, and anterior to it is the adhesive array of 3 lateral ampullae along each side of the 3 median adhesive organs. The tail is wound about halfway around the trunk. An ocellus and an otolith are present in the sensory vesicle. The opaque granular bodies (often found in the larval test of *Lissoclinum* spp., (e.g. *L. conchylium*, *L. badium*) are present in the test, including that around the tail. They are interrupted (leaving clear test) over the sensory vesicle, and separately in front of each adhesive organ.

REMARKS. The vast cloacal space with zooids slung across it in their own test sheath, and the opaque larval test inclusions are found in many *Lissoclinum* spp. An undivided testis and similar small burr-like spicules occur in *L. limosum* and in *L. roseum*, although in both species the spicules are present only in a close capsule around the zooids. Both species are further distinguished from the present one by their relatively soft mucus-like test and their larvae; *L. roseum* having 6 larval ectodermal ampullae and *L. limosum* 10, and in both the larval trunk is nearly 1mm long. *L. badium* also has small burr-like spicules, but it has 2 testis follicles and its larvae are larger with more adhesive organs.

Lissoclinum multifidum (Sluiter, 1909)
(Fig. 141A–C)

Leptoclinum multifidum Sluiter, 1909: 83.
Diplosoma multifidum: Millar, 1975: 238.
Polysoma testiculatum Kott, 1983: 16.

PREVIOUSLY RECORDED. Northern Territory (Port Essington – QM GH802 Kott, 1983). Indonesia (Sluiter, 1909, Millar, 1975). Gulf of Thailand (Millar, 1975). Mauritius (Millar, 1975).

COLONY. Colonies are thin sheets, to 3cm in maximum dimension and to 3mm thick. A few large, sessile cloacal apertures are randomly distributed over the surface. Deep cloacal cavities beneath the apertures extend into deep canals that surround clumps of zooids. Secondary cavities penetrate into each clump to surround the thoraces. Abdomina always are embedded in the basal test. The test is translucent, without any spicules but with some morula bodies. A ring of regularly spaced vesicles surrounds each branchial aperture.

ZOOIDS. Zooids have the abdomen flexed ventrally up against the posterior part of the right side of the thorax. Zooids are about 1mm long with the abdomen in this flexed position. The branchial siphon is small, with 6 sharply pointed lobes around the rim of the aperture. A robust retractor muscle, projects from the posterior end of the thorax. The atrial aperture is large, exposing most of the branchial sac to the cloacal cavity. In the branchial sac 10 stigmata are in the anterior row, 9 in the second, 8 in the third and 7 in the last row. The oesophageal neck is moderately long. The oesophagus is bent through about 130° with the flexure of the abdomen, although the rectum is curved in a more obtuse angle, the right (proximal) part of the gut loop being higher (against the right side of the thorax) than its distal end. The oesophagus, small almost quadrate stomach, and long duodenum comprise the proximal (descending) limb of the gut loop, the oval posterior stomach is in the pole of the loop and the long rectum (constricted partway along its length) forms the distal (ascending) limb. The testis, behind the flexed part of the gut loop, is divided into a circle of 6 pyriform follicles, their narrow ends directed into the centre where they join the vas deferens. Larvae are present in the paratype (QM GH802) collected in June. The almost spherical larval trunk is 0.6mm long. Three ectodermal ampullae are on each side of the base of 3 median adhesive organs at the anterior end of the trunk. An oozooid and one blastozooid are about halfway along the trunk.

REMARKS. The species is distinguished from the temperate *L. concavum* (which has a similarly flexed abdomen and equally numerous testis follicles) by the absence of spicules. The New Caledonian *L. cornutum* Monniot, 1992 and *L. polyorchis* Monniot, 1992 also have a divided testis and the latter species has a ventrally flexed abdomen. However both have large conspicuously stellate spicules.

Sluiter (1909) appears to have confused the muscular retractor muscle projecting into the test from the posterior end of the thorax with a vascular appendage; and, as Millar (1975) observed, his interpretation of the atrial aperture is wrong. Otherwise the zooids and colonies of the specimens described by Sluiter (1909) and Millar (1975) are the same. *L. testiculatum* (Kott, 1983), including the larvae, are also like the specimens described by Millar (1975), although the large cells from the larval haemocoele that Millar found in the specimen from Banda have not been detected in specimen from northern Australia.

Although originally assigned to *Diplosoma*, *L. multitestis* (Monniot & Monniot, 1996) is a member of the *aureum* group with the oozooid halfway along the larval trunk and a multiplicity of testis follicles behind the ventrally flexed gut loop. The species is distinguished from the present one by its larger zooids (including more stigmata) and larvae (which lack a blastozooid), the gastric vesicle between the tubules of the gland and the duct, a relatively small atrial aperture and absence of a retractor muscle. Although Monniot & Monniot (1996) suggested that a difference in the cloacal systems distinguish the species, there is no appreciable difference between the cloacal systems of *L. multitestis* and the present species.

Lissoclinum nebulosum Monniot & Monniot, 1996
(Figs 141D,E, 177E; Pl. 19E,F)

Lissoclinum nebulosum Monniot & Monniot, 1996: 173.

NEW RECORDS. Queensland (Wistari Reef, QM G308011; Heron I., QM G301576; Whitsunday Is, QM G302923).

PREVIOUSLY RECORDED. Federated States of Micronesia (Chuuk Lagoon – Monniot & Monniot, 1996: 173).

COLONY. The newly recorded colonies are gelatinous oval mats to about 4cm long with an even, rounded margin. A thick superficial bladder cell layer contains black pigment cells in life although these are not evident in an in situ photograph (of QM G302992). In preservative,

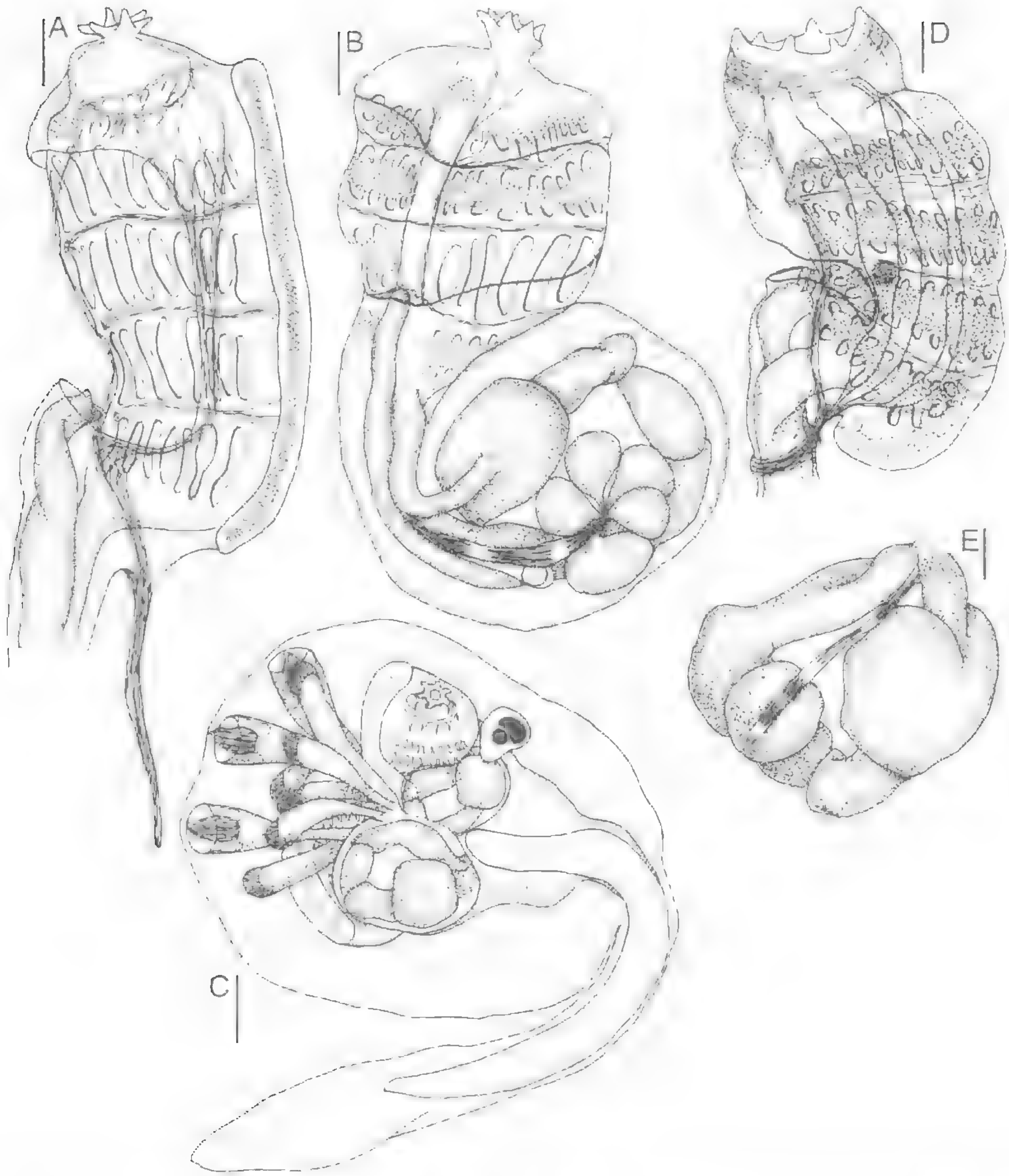


FIG. 141. A–C, *Lissoclinum multifidum* (QM GH802) – A, thorax showing thoracic muscles and retractor; B, zooid; C, larva with thoracic and abdominal buds on right and left respectively. D, E, *Lissoclinum nebulosum* (QM G308011) – D, thorax; E, abdomen. Scales: 0.1mm.

the pigment cells are brown at first, but subsequently all colour is lost in the preserved material. The test is very tough. Spicules are present beneath the bladder cell layer and project up into it around the branchial apertures of the zooids. They are relatively sparse and patchy. In one colony (QM G308011), spicules are not present elsewhere although in another specimen (a fragment of a colony) some are scattered sparsely around the zooids (QM G301576). A colony from the Whitsunday Is (QM G302923) has a capsule of spicules around each abdomen and a strip along the ventrum of each thorax. Spicules are always absent around the rims of the

common cloacal apertures. Zooids open on the upper surface, around the rounded margin of the colony and sometimes over onto the under surface. Randomly distributed common cloacal apertures are on the upper surface and sometimes around the border of the colony. Primary cloacal cavities are very extensive, posterior abdominal spaces separating the upper zooid-bearing part from the spicule-free basal layer. On the side where the zooids have grown over onto the under surface, the cloacal cavity also continues around so that the basal test, surrounded by cloacal cavity, appears to penetrate the colony to separate the zooids on the upper surface from those on the under surface. Shallow secondary cloacal cavities penetrate the surface test amongst the thoraces. Other canals that extend the full length of the zooids connect these thoracic spaces with the posterior abdominal ones. The whole length of the zooids, with the abdomen bent up to the right against the posterior half of the thorax, is embedded in the surface layer of test. Only occasional connectives attach the surface to the basal test. One or two yellow eggs are in some of these connectives.

Spicules, to 0.07mm in maximum dimension have numerous rod-shaped rays composed of needle-like crystals and they disintegrate readily. The rays progressively lengthen to form the points of diamond or square and occasionally fusiform outlines. Some of the spicules are hollow in the centre. *Prochloron* is in patches on the surface of the colony.

Colonies from Micronesia were grey to brown, becoming orange in preservative, but otherwise are like the colonies described above.

ZOOIDS. Zooids are about 1.3mm long, the thorax and abdomen usually of about equal length although relaxed thoraces are 1mm or more long. Zooids are difficult to remove from the test. Branchial apertures have 6 small sharply pointed triangular lobes around each rim. Crowded columnar epithelial cells project from the anterior part of the thorax. The branchial sphincter is very strong. About 5 longitudinal thoracic muscles in the parietal body wall also are strong. The dorsal longitudinal pharyngeal muscles join with the longitudinal parietal muscles at the end of the thorax to form a circular muscle around the oesophageal neck just posterior to the thorax. A retractor muscle does not project away from the zooid. An atrial lip was not detected. The atrial aperture is large, often exposing the whole of the branchial sac. A lateral organ is on the edge of the atrial aperture about half-way down each side. Its position in relation to the atrial aperture depends on the extent to which the sides of the opening are drawn back toward the endostyle. The branchial tentacles, as reported by Monniot & Monniot (1996), are particularly numerous (about 24). In the branchial sac, 12 long stigmata are in the first 2 rows, but only 10 are in the last row. The oesophageal neck is not long in this species, and it bends to bring the abdomen horizontally across the posterior half of the right side of the thorax. The gut forms a narrow curved loop, with a long roomy duodenum, a long balloon-like, oval posterior stomach, sharply constricted off from both the duodenum and the rectum. A distinct rectal valve is at the junction of the posterior stomach and rectum. An oval chamber at the proximal end of the rectum is separated from the distal part by a sharp constriction.

Newly recorded colonies have yellow spherical probably fertilised eggs in the test strands posterior to the zooids. These may be moving into the basal test where embryos, each surrounded by a capsule of spicules, are being incubated in the colonies from Micronesia (see Monniot & Monniot, 1996). The larval trunk is 1.3mm long and a ring of 10 to 20 irregularly spaced ectodermal ampulla encircle the 3 antero-median adhesive organs.

REMARKS. The firm, gelatinous colony, with its vast posterior abdominal cloacal cavity, rather irregular spicules, oesophageal sphincter and large number of larval ampullae are all distinctive characters. The large rather delicate thorax with its strong longitudinal muscles and its flap-like lateral organ, sometimes drawn right back to the endostyle is characteristic of *Lissoclinum*.

An oesophageal constrictor muscle, homologous with the one in this species, occurs in *Didemnum*, *Trididemnum* and *Diplosoma* (see above, Didemnidae). It does not indicate any intra-generic or higher level phylogeny and may have evolved independently in each of the 4 genera in which it occurs, although it could be ephemeral, associated with the process of replication.

The spicules resemble those of *L. vulgare* Monniot, 1992, although they are larger, with more numerous and finer rays. Spicules of *L. calycis*, *L. taratara* and *L. triangulum* have some similarities with those of present species and usually are found encapsulating the zooids and larvae. However, they have even finer spicule rays, and softer colonies without a bladder cell

layer. *L. calycis* has spicules with compact tetrahedral points more distinctly formed and differentiated from the shorter, finer needle-like rays in the centre of the spicules; and in *L. triangulum* the spicules are more flattened. *L. taratara* has thicker and fewer spicule rays and its spicules are larger. *Didemnum uturoa* has a superficial resemblance to the present species with dark pigment in a thick bladder cell layer and similar spicules (albeit with thicker, flat-tipped rays) crowded in the basal test. It does not have such extensive cloacal cavities.

Monniot & Monniot (1996) reported absent the branchial sphincter, which is strongly developed in the newly recorded Australian material.

Lissoclinum ostrearium (Michaelsen, 1930) (Figs 142, 176E)

Diplosomoides ostrearium Michaelsen, 1930: 526.
Leptoclinum (*Lissoclinum*) *ostrearium*: Kott, 1962: 308.
Lissoclinum ostrearium: Kott, 1976: 71; 1998: 87.

NEW RECORDS. Western Australia (Cockburn Sound, WAM 199.91). South Australia (Great Australian Bight, SAM E2631; Wright I., exposed side, SAM E2668).

PREVIOUSLY RECORDED. Western Australia (Rottnest I. – Kott, 1962; Cockburn Sound, Albany – Michaelsen 1930). South Australia (St Vincents Gulf – AM U3986 Kott, 1962). Victoria (Western Port – Kott, 1976).

COLONY. Colonies are flat sheets with a smooth surface perforated by the regularly stellate branchial apertures. Spicules are absent from a circular area around each branchial opening although a few are in the siphonal lining. Otherwise the surface test has crowded spicules and sometimes minute, crowded, spicule filled papillae project from the surface. Spicules are present throughout the colony, although they are not packed hard — they are not as crowded in the internal test as in the surface and base — and the colony is flexible. Spicules are burr-like, to 0.03mm diameter but usually less, with 17–19 long needle- and rod-like rays in optical transverse section, sometimes with irregular or rounded tips. The brownish zooids surrounded by brown spherical cells are clearly seen in the test strands that cross the vast cloacal cavity between the thin surface and basal layers of test. Thin test connectives sometimes enclose a clump of 2 to 4 abdomina, but they subdivide at thorax level, each thorax having a separate ventral sheath of test. Sometimes the test connective branches to separate whole zooids from one another. Common cloacal apertures are large, open, slightly gathered around the rim, and randomly distributed over the surface.

ZOOIDS. Zooids are delicate, to 1mm long but the post-pyloric part of the abdomen is bent up at right angles to the long axis of the zooid. The thorax is long and not very contractile and the rectangular stigmata are long. The branchial siphon is short, with 6 narrow, pointed finger-like lobes around the rim. The atrial aperture is large exposing most of the branchial sac directly to the cloacal cavity and an atrial tongue projects from the anterior rim. A retractor muscle was not detected. The oesophageal neck is long and curved. The post-pyloric part of the gut loop consists of the usual duodenum, posterior stomach, and long rectum. The vas deferens curves around the outer surface between the two testis follicles at the posterior end of the zooid (against the ventral flexure of the gut loop) and extends anteriorly with the rectum.

Larvae are present in colonies from Port Naorlunga (S.A.) taken in January. They have a trunk 0.7mm long with 4 club-shaped lateral epidermal ampullae along each side of the 3 antero-median adhesive organs. The cerebral vesicle contains ocellus and otolith. The larval test contains a single layer of crowded circular to polygonal cells to 0.014mm diameter containing evenly distributed granules. These are interrupted over the cerebral vesicle and in front of each of the adhesive organs. They are not likely to be blood cells being in the larval test rather than the haemocoel, nor are they spicules as Kott (1962) suggested.

REMARKS. The species is distinguished from the sympatric *L. durabile* by its smaller spicules (to 0.03mm diameter rather than 0.05mm) and vast common cloacal cavity, the abdomina being partially or completely free of the basal layer of test and never completely embedded in it. The cloacal cavity of the other sympatric species, *L. concavum*, is deep but is broken up into separate systems, it has fewer and often flat-tipped spicule rays (unlike the chrysanthemum-like spicules of the present species), its spicules are absent from an area around the branchial apertures and it has numerous testis follicles. Further, in the present species the branchial apertures are at the surface rather than being depressed into it as they are in *L. concavum*.

The extensive cloacal cavity of the present species resembles the tropical *L. badium* and *L. reginum*. These species have spicules with more and finer rays, some exceeding the maximum diameter of spicules of the present species. The granular bodies in the larval test

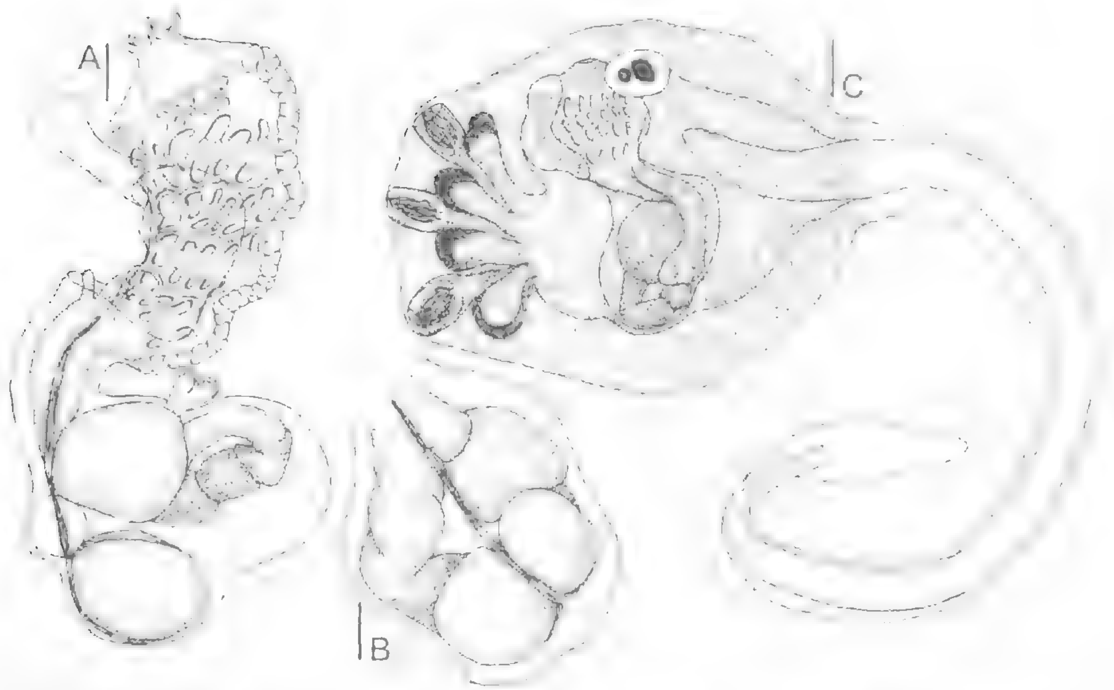


FIG. 142. *Lissoclinum ostrearium* (A, SAM E2631; B, SAM E2668; C, AM U3986) – A, zooid; B, abdomen showing testis and vas deferens; C, larva with opaque cells embedded in the test of the trunk and terminal columnar cells over the tips of the ectodermal ampullae. Scales: 0.1mm.

occur also in *L. fragile* Van Name, 1902, *L. japonicum* Tokioka, 1958, *L. reginum*, *L. badium* and *L. caliginosum*.

Lissoclinum patella (Gottschaldt, 1898)
(Figs 143A,B, 178B; Pl. 19G,H)

Didemnoides patella Gottschaldt, 1898: 653.
Didemnum patella: Michaelsen, 1920: 63. Tokioka, 1950: 115. Millar, 1975: 228.
Leptoclinum patella: Kott, 1962: 310.
Lissoclinum patella: Tokioka, 1967: 97. Kott, 1977: 619; 1980: 18; 1981: 189; 1982a: 113; 1998: 88. Parry, 1987: 113. Monniot & Monniot, 1987: 52; 1996: 174. Monniot, 1992: 572.
Not *Didemnum patella*: Millar, 1963: 701 (< *L. bistratum*).
Didemnoides ternatanum Gottschaldt, 1898: 648.
Not *Didemnum ternatanum*: Van Name, 1918: 152. Tokioka, 1955: 47; 1967: 77. Tokioka & Nishikawa, 1975: 326. Kott, 1966: 287; 1977: 618. Vasseur, 1970: 213. Newcomb & Pugh, 1975: 533. Millar, 1975: 229 (< *Didemnum molle*).
Didemnoides sulcatum Gottschaldt, 1898: 651.
Didemnum meandrium Sluiter, 1909: 64.

NEW RECORDS. Western Australia (Montebello Is, QM G302905; Kimberley, WAM 766.91). Queensland (Capricorn Group, QM G302984; Swain Reefs, QM G305714; Bowden Reef, QM G300974; Tydeman Reef, QM G300959). Eastern New Britain (QM G300945).

PREVIOUSLY RECORDED. Western Australia (Cockburn Sound – AM Y1335 Kott, 1962). Queensland (Heron I., Swain Reefs – QM G9278, G9456, G9887, GH1353, GH1415, GH1835, GH3047, Kott, 1962 1977 1980; Lizard I. – QM GH125, GH3825, GH3836; Tijou Reef – Kott, 1982a). Coral Sea (Chesterfield Reef, Monniot, 1992). Indonesia (ZMH K1087 holotype *D. patella* Gottschaldt, 1898; ZMH K595 holotype *D.ternatanum* Gottschaldt, 1898; ZMA TU457, TU459 syntypes *D.meandrium* Sluiter, 1909; Millar, 1975). Philippines (Van Name, 1918; Kott, 1982a). Borneo (Sluiter, 1909). Guam (Kott, 1982a). Palau Is (USNM 11419, 11637, 11664, 11688 Tokioka, 1950, 1967; Kott, 1980). New Caledonia (Monniot, 1992). French Polynesia (Monniot & Monniot, 1987). West Indian Ocean (Michaelsen, 1920).

Although Kott (1980, 1981) believed that this species did not occur intertidally, it does occur in shallow reef flat habitats at most locations as well as at greater depths to 10m. Monniot & Monniot (1987) referred to the species being taken always with *Diplosoma similis*. However, the large fleshy colonies of this species are seldom found in the same cryptic habitats that the relatively thin encrusting colonies of *D. similis* favour. The present species is seldom found in cryptic habitats — it is more often found on the open reef flat or on the slope.

COLONY. Colonies form large, gelatinous translucent, greenish-grey masses, up to 5cm or more thick, and sometimes almost 1m in greatest dimension. High gelatinous spicule-free ridges on the upper half of the colony are of about the same height as the thickness of the lower half, and

the thin zooid-bearing layer is between the two. The high rounded ridges of test surround narrow, deep depressions or pits penetrating to the zooid layer. The zooids open into the base of these pits. A white line along the centre of the surface ridges appears to be a test vessel just beneath the surface. Deep common cloacal canals, surround clumps of zooids and extend posterior to them. Shallower canals penetrate clumps of zooids at thoracic level.

Prochloron are in the cloacal cavities and, seen through the translucent test, confer a greenish tinge to the living colonies. The bright green colour of the *Prochloron* can be seen through the thin layer of test over the zooids at the base of the pits on the upper surface. A vertical cut through the colony along a high gelatinous ridge will display the thin, bright green horizontal layer of *Prochloron* halfway down. The branchial apertures are longitudinal slits with clumps of white spicules at each end where the test intrudes between the anterior and posterior lips of the apertures. Spicules, in the central (zooid) layer of test, are spherical, with crowded, flat-tipped radiating rays. They range in size from from 0.01 to 0.08mm in diameter, the various sizes being present in about equal proportions.

Smaller colonies, to about 5cm diameter in greatest dimension (QM G302905) are regular circular to oval mats about 5mm thick with a smooth rounded outer margin. Only one common cloacal aperture is present, in the centre of the upper surface which is smooth and almost even. There are no marked gelatinous ridges although shallow circular surface elevations, caused by a thickening of the superficial bladder cell layer, are present. They are surrounded by depressions over circular primary common cloacal canals, lined on each side by zooids. In preserved specimens, long branchial siphons are seen projecting through the superficial bladder cell layer surrounded by 6 groups of spicules from the underlying spicule layer. In these relatively small, flat colonies, loose sand and small rubble particles on the base are consistent with the colonies lying on a flat, sandy surface. The spicules are in a layer that lies beneath the superficial bladder cells and curves around the sides of the colony, becoming continuous with a layer in the floor of the posterior abdominal common cloacal cavities which extend from the deep primary canals.

ZOOIDS. Zooids are relatively large, to about 3mm overall. The thorax is particularly long, with long rectangular stigmata, 12 in the anterior row reducing to 9 in the posterior row. The abdomen and branchial sac are about equal in length and the branchial siphon is half that length. The rim of the branchial aperture has 6 small pointed lobes around it, although these often are obscured by the arrangement of the siphonal muscles which modify the opening into a longitudinal slit. A false siphon is present in the base of the branchial siphon, projecting sometimes as much as halfway up the length of the siphon. Stout branchial tentacles are in its base. In a few zooids (QM G302905) the internal (false) siphon is invaginated into the branchial sac and the branchial tentacles are between the branchial wall and the internal wall of the false siphon, thus isolated from the incurrent stream of water. The atrial aperture is wide open, exposing most of the branchial sac directly to the cloacal cavity. A lateral organ is present about one-third of the way down each side of the atrial opening (on each side of the endostyle). From the base of the oesophagus the gut loop is often bent ventrally at right angles to the vertical axis of the zooid although in other colonies it is a long vertical loop. The undivided testis lies behind the flexed part of the gut loop, or at the posterior end of the abdomen, with the straight vas deferens hooked around it.

Embryos are being incubated in the basal test of colonies collected from Lizard I. in April (QM GH3825), and Cockburn Sound in January (AM Y1335). They are not recorded from other locations. Monniot & Monniot (1987) refer to the characteristic *Lissoclinum* larvae with 4 rows of stigmata in the oozooid. However, it is not clear that the larvae referred to are from the French Polynesian material or whether the reference is to those recorded from Western Australia (Kott, 1962, 1980). Larvae of characteristic size and form are figured (Monniot, 1992) from the New Caledonian or Chesterfield Reef specimens — neither date nor location is given. Larvae are large, almost spherical, the trunk to 2.5mm long with a short tail extending only about two-thirds of the way along its ventral border. The 3 antero-median adhesive organs have short stalks and large axillary cones in a shallow epidermal cup. The anterior end of the trunk, around the base of the adhesive organs, is produced forward into about 30 short ectodermal ampullae. An oozooid and a blastozooid are present about halfway along the trunk, each with 4 rows of stigmata. *Prochloron* cells adhere to the test around the posterior third of the trunk where it narrows (behind the oozooid and blastozooid). The sensory vesicle protrudes from the upper border of the oozooid.

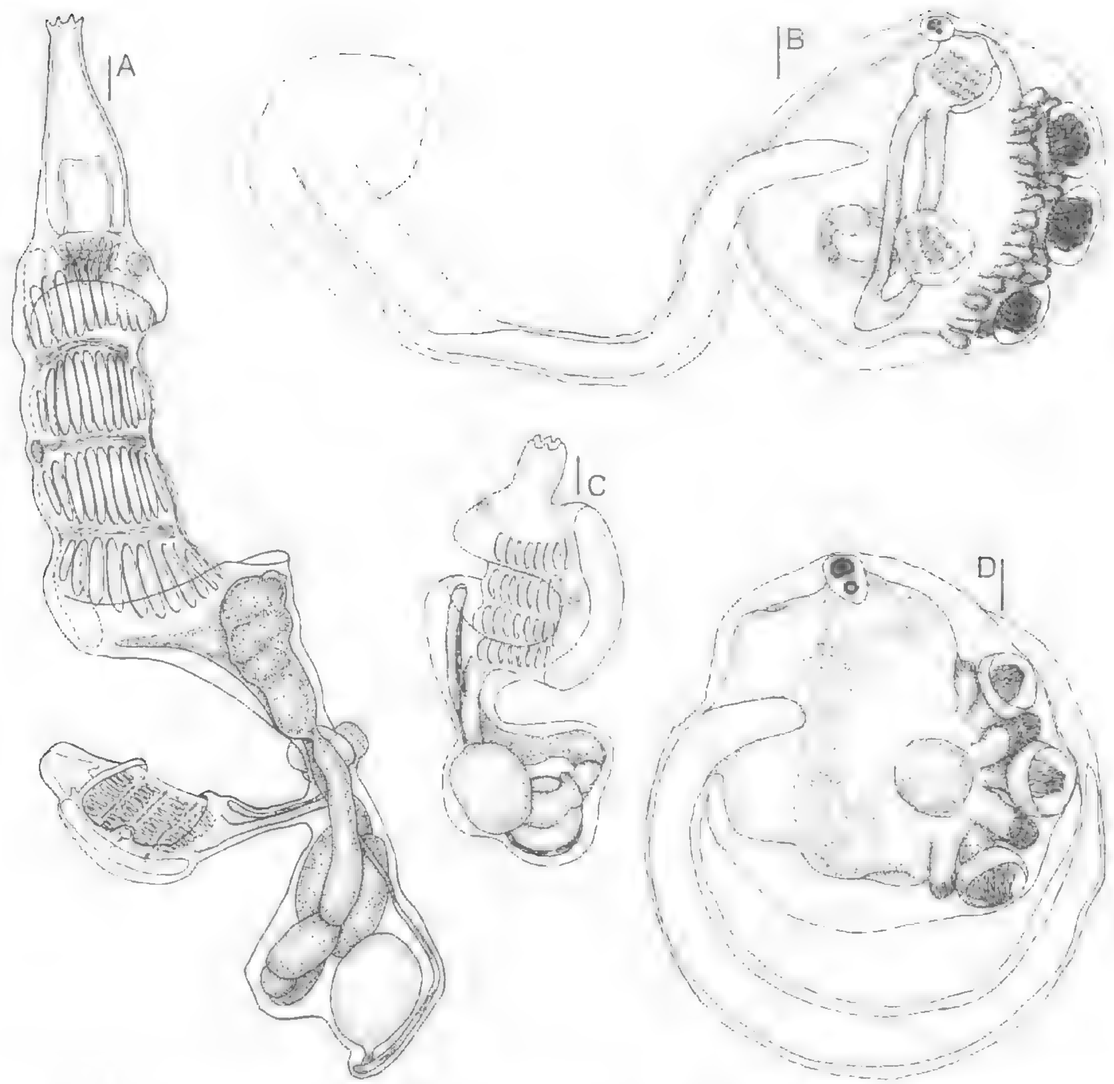


FIG. 143. A,B. *Lissoclinum patella* (A, QM G302905; B, AM Y1335) – A, zooid; B, larva with an abdominal and a thoracic bud. C,D, *Lissoclinum punctatum* (C, QM G12452; D, QM G308041) – C, zooid; D, larva, adult organs not well advanced. Scales. A, B, 0.2mm; C, D, 0.1mm.

REMARKS. The gelatinous colony, large larvae and zooids, long branchial siphon, false siphons and the great range in spicule diameter are distinctive and the species is readily identified.

L. patella shares with *L. bistratum* and *L. timorense* the 2-lipped branchial apertures and larvae with numerous short ectodermal ampullae around the anterior end of the trunk and *Prochloron* adhering to the test around the posterior third where it narrows toward the tail. However, these species have neither the large gelatinous colonies of the present species nor its large zooids and long branchial siphons with a false siphon in their base. *L. timorense* also has different spicules and surface papillae. The smaller flat plate-like colonies of the present species do resemble some large *L. bistratum* colonies — they both have globular spicules with numerous flat-tipped rays, and occupy the same reef flat habitats. However, *L. bistratum* colonies usually are smaller, have only a thin surface bladder cell layer, an even upper surface, carotenoid pigments (that appear not to be in the present species) and smaller spicules never more than 0.05mm diameter

The green-grey translucent colonies are difficult to see in situ, despite their non-cryptic habitats and large size. This may partly be the explanation for the relatively few records of this very common species. Also the species is so readily identified in the field that specimens tend not to be collected and remain unrecorded.

Monniot (1992) refers to the infrequent occurrence of larvae. Before newly recorded specimens from Lizard I. were found to contain them, Kott's (1962) specimen from Cockburn Sound (Western Australia) and Monniot's (1992) from the western Pacific were the only larvae reported. The fact that specimens are readily identified thus removing the necessity to dissect, or even collect them for species identification, does not seem to be the reason for the lack of larvae. Although only 14 specimens are in the Queensland Museum collection (all from some part of the Great Barrier Reef) some could be expected to contain larvae for they generally are large and were collected over most of the year — in January, March, April, June, August, September, October and December. Nevertheless embryos are present only in the Lizard I. colonies collected in April. At this stage it is possible that each colony may have a limited reproductive season, possibly only once annually.

It is probable that poor descriptions (confined to the most conspicuous characters) may also result from the fact that the species is so readily identified. For instance, the false siphon, presently known only in this species and in the *dubius* group of *Leptoclindes* has not previously been reported. The functional significance of this structure is not known although it could be associated with a reef flat habitat, and the occasional invagination of the structure could be to ensure the irrigation of the groove between the outer siphon and the inner false siphon where sediments could settle. Its invagination into the pharynx does not appear to be a consistent position for the false siphon, and since it isolates the branchial tentacles from the direct incurrent stream, it is not likely to occur often.

The synonymy set out above is based on re-examination of material described by Gottschaldt (1898) in Hamburg Zoological Museum and by Sluiter in the Zoological Museum, University of Amsterdam. Although the name *Didemnoides ternatanum* Gottschaldt, 1898 has page priority over *D. patella* Gottschaldt, 1898, Kott (1980) established *D. patella* as the senior synonym.

Lissoclinum punctatum Kott, 1977
(Figs 143C,D, 175-I)

Lissoclinum punctatum Kott, 1977: 620; 1980: 20; 1981: 198; 1982a: 114; 1998: 88. Monniot, 1992: 575.
Lissoclinum molle: Newcomb & Pugh, 1975: 533.

NEW RECORDS. Queensland (Capricorn Group, QM GH3498, G308041; Hardy Reef, QM GH2072; Lizard I QM GH5290; far northern Great Barrier Reef, QM GH5357).

PREVIOUSLY RECORDED. Queensland (Capricorn Group to Lizard I. – Kott, 1977, 1980). West Pacific (Palau Is – Kott, 1982a; Fiji – QM G12452 Kott, 1980; New Caledonia – Monniot, 1992). Singapore (Kott, 1982a).

COLONY. Colonies are small and very soft. When undisturbed they form irregular, thin cushions about 2mm thick and up to 2cm long on hard substrates. They are mostly bright green owing to the *Prochloron* cells in the common cloacal cavity although a translucent whitish outer margin of test into which the common cloacal canals and green *Prochloron* do not penetrate is around each colony. When attempts are made to remove them from the substrate or the test is manipulated in any way, it disintegrates into almost liquid mucus-like material and mixes with the green cells. The common cloacal cavity is large, extending posterior to the zooids in the upper half of colony. It does not extend into the lower half.

Zooids (both abdomen and thorax) and developing embryos and larvae are enclosed in capsules of white spicules. Spicules are not present elsewhere in the test. They are spherical, 0.01–0.03mm in diameter with flat-ended rod-like rays.

ZOOIDS. Zooids are small, about 1mm long. The cylindrical branchial siphon has 6 shallow lobes around the aperture. The atrial aperture is wide, exposing most of the branchial sac directly to the common cloaca and there is virtually no peribranchial cavity. There is no atrial lip. Fine longitudinal parietal muscles extend onto the oesophagus but do not form a retractor muscle. About 8 narrow stigmata are in each of the 4 rows in the branchial sac. A small lateral organ is on each side of the endostyle about halfway down the thorax. The simple gut loop bends ventrally at the oesophageal neck and lies at right angles to the long axis of the thorax. The descending limb of the gut loop consists of oesophagus, stomach and a short duodenum. The posterior stomach is in the pole of the gut loop. An undivided testis is beneath the flexure of the gut loop, and the proximal end of the otherwise straight vas deferens curves around the testis.

Fertile eggs are isolated from the side of the abdomen and embryos, enclosed in a capsule of spicules, are brooded in the test. Tailed (but not well advanced) larvae were present in Fijian material in July. However larvae were not found in specimens taken in January, May, June, August, September and October at various locations in the Great Barrier Reef, nor in June at Lizard I. Monniot (1992) found larvae in specimens from New Caledonia although the date they were collected is not published. They also have been taken in newly recorded specimens from Wistari Reef collected in March (QM G308041). They are relatively large, the trunk 0.7mm long with the tail wound halfway around it. Anteriorly, on each side of the 3 large adhesive organs, are 4 lateral ampullae with rounded tips. The cerebral vesicle protrudes from the dorsal surface and one blastozooid in addition to the oozooid are developing about halfway along the trunk. The pharynges of blastozooids and oozooids have 4 rows of stigmata. Thoracic and abdominal buds have a separate origin from the base and top respectively of the long oesophageal neck of the oozoid, although this is not shown for the New Caledonian specimens (Monniot, 1992: figs 5B,C) in which the stigmata have not perforated the pharynx in either the oozooid or blastozooid, even though the larvae appear to be well advanced. They are otherwise similar to those from Wistari Reef with particularly large adhesive organs, a protruding cerebral vesicle, and the tail wound halfway around the trunk which is 0.6–0.75mm long. Larvae from Uié Bay (Monniot, 1992) with 2 adhesive organs and 2 pairs of lateral ampullae may not belong to this species.

Despite the rare occasions on which larvae have been taken, it is not likely that breeding seasons are also rare — for the presence of these small colonies indicates that settlement occurs throughout the year. It is not likely that these small, vulnerable colonies have long life spans, particularly in the rubble zone, where habitats are unstable. It is more likely that incubation is rapid and that larvae are rapidly released.

REMARKS. The small and very soft, bright green colonies, with their zooids enclosed in white capsules, are unique and a common component of the cryptic fauna around the base of coral colonies and amongst rubble. The small spherical spicules with rod-like rays resemble others in *Lissoclinum*. A similar spicule distribution (confined to the capsules around zooids and larvae) occurs in *L. triangulum*, *L. mereti*, *L. tasmanense*, *L. ravarava*, *L. pacificense*, *L. calycis* and *L. verrilli*. Of these species, only *L. triangulum* has green plant cell symbionts, but these are embedded in the test, rather than in the cloacal cavity, and the spicules themselves are not spherical — they have rays of different lengths, as do the other species listed that form capsules around the zooids.

The identity of New Caledonian colonies assigned to this species (Monniot, 1992) needs confirmation as, apart from the possible blastozooids, the larvae appear to be identical with those of *Trididemnum cyclops*.

Calcareous spicules also form capsules around the zooids in *Cystodytes* and *Eucoelium* (>*Polycitorella*) of the Polycitoridae, but a direct relationship between Didemnidae and Polycitoridae is not implied by this character.

Hirose et al. (1996) found some phagositised *Prochloron* cells in test cells around the common cloacal cavity. This is more likely a response to the penetration of symbionts into the test (where they usually do not occur) than an example of stable endosymbiosis and a model for the evolution of the ancestral green plastid which these authors propose it to be.

Lissoclinum reginum sp. nov.
(Figs 144, 176G; Pl. 20A–D)

Diplosomoides ostrearium: Hastings, 1931: 104.
?*Lissoclinum fragile*: Monniot & Monniot, 1987: 49.

TYPE LOCALITY. Queensland (Heron I., eastern end, below low tide, coll. P.Kott 09.03.93, holotype G308077: on *Halimeda* sp., paratypes QM G308088).

FURTHER RECORDS. Queensland (Capricorn Group, QM G9419, G302073, G302109, G302142, G302425, G302982, G308025, G308037, G308070-1, G308076, G308086-7, G308252, G308281, G308300-2, G308320, G308322-3, G308325, G308345, G308476; Swain Reefs, QM G305456, G305800, G308381; Lizard I., QM G302487). Indian Ocean (Cocos Keeling, WAM 611.89 613.89).

COLONY. In life some small colonies are regular oval to irregular, magenta[R] coloured plates or strips on *Halimeda* or coral rubble. Larger colonies are extensive (up to 0.5m) sheets stretched thinly over the bases of coral boulders. They are flax-flower blue[R], violet[R], magenta[R], prune-purple[R], plum-purple[R] or slate grey[R], sometimes with much of the upper surface dirty white or drab brown with pigment uneven, concentrated near the outer margins or around the zooid openings or in patches on the surface. Actual margins of the colony are white with crowded spicules and lack pigment. Pigment

cells are confined to a thin surface layer of test, mixed with and superficial to the spicules. In preservative the purple pigment changes to blackish brown with some orange pigment cells. Colonies at first look brown, pinkish-brown or beige, depending on the distribution of pigment and spicules in the upper surface. In preservative, zooids are a translucent brownish colour with brown and yellow pigmented cells in the haemocoel the brown colour can be seen through the open branchial apertures. After a long period in preservative, colonies become white. The preservative is stained a yellowish-brown colour. Large reservoirs of pigment are in the basal test, as if withdrawn from the surface.

Colonies are attached loosely to the substrate and tend to grow over rubble rather than around it. Smaller plates have attachment processes stretching out around the margins of the colony. Large sheets are difficult to remove entire because they are so thin and fragile, not because they are particularly well attached. Living colonies appear to be thicker than preserved ones because the excurrent water in the vast common cloacal cavities inflates the colony. Water pressure also keeps the large common cloacal apertures raised above the otherwise smooth upper surface. Common cloacal apertures, when fully distended, often are large (to 5mm diameter). In preserved specimens these often are long slits. Branchial apertures are circular without spicules around their rims.

Only the anterior part of the zooid is embedded in the surface test. Abdomina sometimes are partially embedded in the basal test, but more often the whole zooid, except the anterior part of the thorax, is suspended vertically in strands of test that cross the common cloacal cavity between the surface and basal layers. One to 3 abdomina are clumped together in a single strand of test with a thin posterior abdominal connective anchoring them to the basal test. Thoraces always are entirely separated from one another, each having a single ventral test strand continuous with the surface test. Larvae protrude, and probably are liberated, into the cloacal cavity from the basal test where they incubated.

Spicules sometimes are fairly evenly distributed throughout, including the strands of test in which the zooids are suspended, although usually fewer spicules are in the surface than in the basal test. The concentration of spicules in the surface test affects the colour — fewer spicules resulting in more intensely coloured colonies. Colonies with moderate concentrations of spicules and sparse pigment superficially appear spotted when spicules are absent over the brown zooids. Most smaller plate-like colonies have a fluffy appearance owing to relatively sparse concentrations of spicules in the often darkly pigmented surface layer of test. Spicules are burr-like and globular, to 0.04mm in diameter but usually less, with long, crowded flat-tipped or occasionally needle-like rays.

ZOOIDS. Zooids are delicate and are not readily removed from the test. The abdomen, especially, is tightly enveloped in test. The branchial siphon is very short, with 6 shallow lobes and a small sphincter. The atrial aperture is vast, the whole branchial sac being exposed directly to the common cloacal cavity. An atrial tongue projects from the upper rim of the opening but this often is broken when the zooid is removed from the colony. Stigmata are large and rectangular, 9 in the anterior row, 8 in the second and third rows and 7 in the last row. The usual dorsal pharyngeal muscles are present, but delicate and difficult to demonstrate. Some fibres extend a little way down each side of the oesophagus and sometimes a very short retractor projects from the anterior part of the oesophagus. The gut forms a wide open loop. Two large testis follicles have a straight vas deferens hooked around them.

Larvae are present in colonies collected in March. Four lateral ampullae are on each side of the 3 antero-median adhesive organs. The latter have deep narrow axillary cones set in particularly deep epidermal cups. The larval trunk is 0.7mm long and the tail is wound halfway around it. The otolith and ocellus are well formed and 4 rows of stigmata are in the larval pharynx. A blastozooid is not present. Oval granular cells are in the larval test, especially around the posterior two-thirds of the trunk. They become less crowded anteriorly.

REMARKS. The colour of the species is distinctive. Although the small fluffy (juvenile ?) magenta colonies look very different from the extensive sheets, actual morphological differences (except those associated with size) have not been detected. One specimen (QM G308302) is a very small, thin smear over the substrate. It lacks pigment altogether. Otherwise no difference from the characteristic purple colonies could be detected, except for some spherical yellow cells creating an iridescence in the branchial vessels. Some of the larger sheets lack pigment in some parts of the surface and

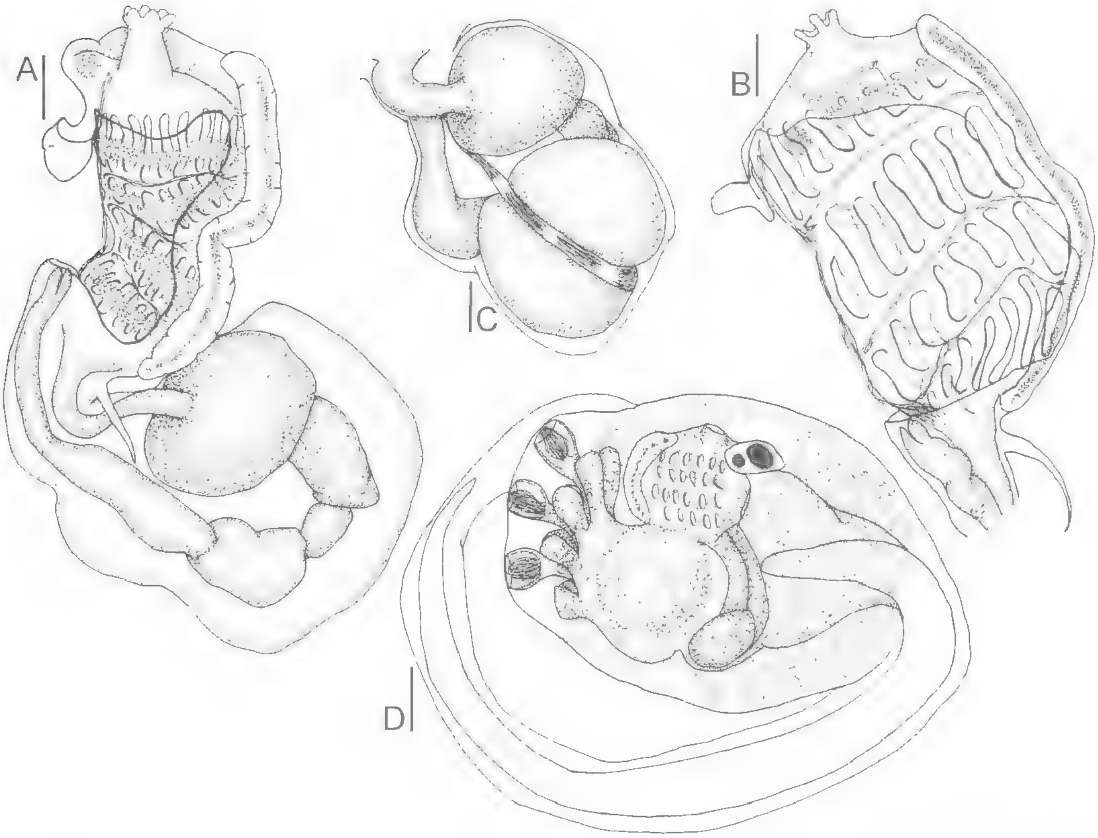


FIG. 144. *Lissoclinum reginum* sp. nov. (A, QM G308325; B, QM G308087; C, QM G308302; D, QM G308077) – A, zooid; B, thorax; C, abdomen from dorsal surface; D, larva. Scales: 0.1mm.

resemble this small, colourless specimen. Fewer spicules have needle-like rays than in the possibly related *L. caliginosum* and *L. badium*. Further, the spicules of the present species are smaller than those of *L. caliginosum* but only slightly larger than those of *L. badium*. The colonies of the present species are also more brittle than the rather rubbery ones of *L. badium* and they lack the spicule-free superficial pigmented surface of *L. caliginosum*. The larvae of the present species have only 3 adhesive organs rather than the 7 or 8 in *L. badium*. The opaque granular bodies in the larval test are less conspicuous than in other species of the *fragile* group.

The specimens assigned to *L. fragile* from 25m in the port of Noumea (Monniot, 1992), some with a small retractor muscle (see also QM G308070, G308087) are said to be white or pink, although it is not clear whether or not this is their colour alive or in preservative. Other recorded characters of colony, zooids and larvae are the same as the present species and they may be conspecific. This is more likely than conspecificity with the Atlantic *L. fragile*, which is characterised by its white, very brittle colonies, orange zooids in life, and conical as well as flat-tipped or needle-like spicule rays (Van Name, 1902, 1921, 1945).

L. ostrearium (Michaelsen, 1930) from southern Australia has smaller spicules with fewer, thicker and less needle-like rays than the tropical *D. ostrearium*: Hastings, 1931. The specimens from Low Is (Hastings, 1931) are reported to have been purple when alive, and to have been growing on a linear leaf. In her description, Hastings (1931) emphasised the differences between this species and *D. molle* (Herdman, 1886) rather than the differences between this and other species of *Lissoclinum*. The large delicate branchial sac with flat epithelial cells lining the stigmata occurs in *L. caliginosum* and *L. badium*. Nevertheless the similarity between its habitat and appearance

(including colour) establishes the Low Is specimens as conspecific with the present colonies taken on the fronds of *Halimeda* sp.

L.vareau Monniot & Monniot, 1987 from French Polynesia and New Caledonia has a similar, thin mauve colony and the testis has 2 follicles, but it differs from the present species in the absence of a retractor muscle and its different larvae (with numerous lateral ampullae).

Lissoclinum roseum sp. nov.
(Figs 145, 176B,C; Pls 4C, 20E,F)

?*Diplosoma ata* Monniot & Monniot, 1987: 57 (part, specimens with 'fibrous annulus').

TYPE LOCALITY. Queensland (Wistari Reef, landing stage, low tide rubble fauna, coll. P. Kott 06.03.93, holotype QM G308053; Heron I. north, opposite cay, Gorgonia Pools, low tide rubble fauna, coll. P. Kott 05.09.94, paratypes QM G308312).

FURTHER RECORDS. Queensland (Hervey Bay, QM G9441, G302091; Capricorn Group, QM G11901, GH2276, G301547, G301555, G302144, G302202, G302324, G302326-9, G302506, G302520, G302553-4, G302557, G302576, G308052-3, G308270, G308309-11; Swain Reefs, QM G308369, G308420).

COLONY. In life, colonies are distinctive soft, low, irregular cushions, sometimes lobed around the rounded margins. Overall they are pink, the test glassy, transparent sometimes vinaceous rufus[R] with pink to scarlet vermilion[R] zooids always encapsulated in white opaque spicules. In life the thoracic capsule of opaque spicules is in 4 parts — one large ventral band, 2 latero-dorsal bands, and a short median dorsal one terminating at the atrial aperture. Uninterrupted capsules of these opaque spicules respectively surround the abdomen and the developing embryos enclosed in a brood pouch attached to the abdomen. Spicules are small (to 0.025mm in diameter) and burr-like with needle-like rays, some slightly longer than others.

The transparent test is very soft and mucus-like. When undisturbed it holds its shape, but when disturbed it disintegrates readily and a layer of this mucus-like test always clings tightly around zooids and embryos and is difficult to remove. Zooids and larvae are embedded in the test. A thoracic cloacal cavity is present but is difficult to display owing to the very soft test. In preservative colonies are less delicate, the test slightly firmer, and both test and zooids are cream.

One colony (QM G302327) is said to have been lemon-yellow in life, although in other respects it is similar to others of this species.

ZOOIDS. Zooids have a larger thorax, about 1mm long when relaxed. The abdomen is bent up at right angles to the long axis of the thorax. The branchial aperture has 6 moderately long pointed lobes around its margin. The atrial aperture is wide open, exposing the branchial sac directly to the cloacal cavity. A muscular annulus is in the body wall of the oesophageal neck and sometimes is very conspicuous. Although its connection with thoracic muscles was not demonstrated, it appears to consist of muscle fibres and is most likely a homologue of a similar muscle in other genera (see Remarks below). Ten long narrow stigmata are in the anterior row of the branchial sac, and these reduce to 8 in the posterior row. The stomach and posterior stomach are yellow-brown in the preserved material, but the remainder of the horizontal gut loop is colourless. An undivided testis is posterior to the gut loop and the straight vas deferens curves around its dorsal margin to extend anteriorly between the rectum and oesophagus to open near the anus.

In specimens collected at Heron I. in March (QM G308053), October (QM G302324) and November (QM G302326), developing embryos are being incubated in brood pouches projecting out from the zooid — from the base of the oesophagus, near the bend of the gut loop behind the oesophageal annulus and in front of the testis. The larva has a trunk 0.9mm long with a short tail wound only around the ventral surface of the trunk. Six lateral ampullae are on each side of the 3 median adhesive organs. An oozooid (with ocellus and otolith in a protuberant cerebral vesicle) and a blastozooid are halfway along the trunk.

REMARKS. The soft, translucent pink cushion-like colonies of this species are common and conspicuous. The inconspicuous spicules encapsulating the zooids, the location of the larval oozooid and blastozooid in the middle of the trunk (rather than at the anterior end as they are in *Diplosoma*) and the relatively large number of epidermal ampullae indicate that the present species belongs in *Lissoclinum*. The species shares some characters with some specimens which may have been erroneously assigned to *Diplosoma ata* Monniot & Monniot, 1987 from French Polynesia and New Caledonia (Monniot, 1994), viz. an undivided testis, a stalked brood pouch attached to the abdomen, a large thorax, the same number (about 10) of long delicate stigmata and an oesophageal sphincter muscle. Generally *D. ata* zooids have a retractor muscle,

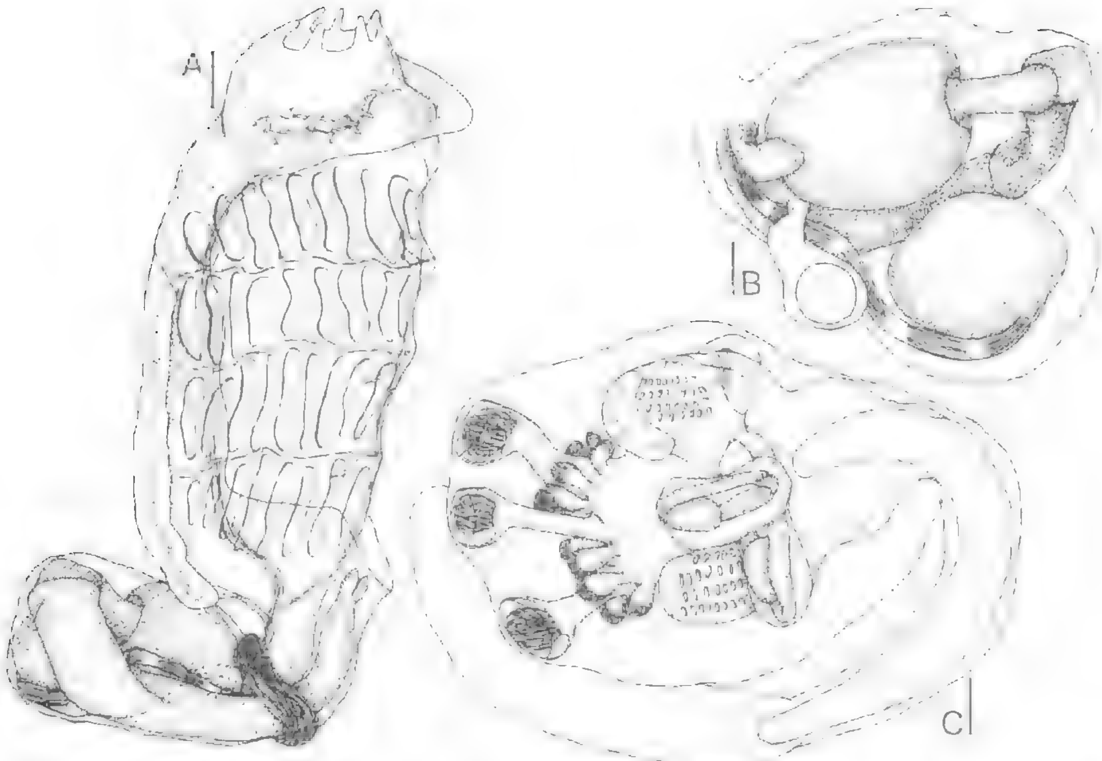


FIG. 145. *Lissoclinum roseum* sp. nov. (A, QM G308312; B, QM G302324; C, QM G308053) – A, zooid showing circum-oesophageal muscle; B, abdomen; C, larva showing abdominal and thoracic buds and terminal columnar cells on tips of ectodermal ampullae. Scales: 0.1mm.

large branchial lobes and larvae characteristic of *Diplosoma* with oozooid and blastozooid at the anterior end of the larval trunk (see *D. ferrugeum*).

Monniot & Monniot (1987) thought the oesophageal annulus was fibrous, and a product of the test. There is no homologue of a fibrous annulus in any ascidian. Careful examination of the structure shows it to be in the body wall (not the test) and to consist of what appear to be circular muscle fibres. It is homologous with a similar structure in *Didemnum fucatum* and *L. nebulosum* (in which its association with the dorsal thoracic muscle has been demonstrated) and probably in *Trididemnum cyclops* (see Monniot & Monniot, 1987).

The species lacks the black pigment of *L. limosum*, and its spicules are more distinctly spherical with more regular rays of even length. *L. ravarava* Monniot & Monniot, 1987 has a similar colony with partially encapsulated zooids but only 2 pairs of larval lateral ampullae (Monniot, 1992) and black pigment in the adult colony.

Lissoclinum sente sp. nov.
(Figs 146A, 177H)

Echinoclinum pacificense Kott, 1981: 193 (part, specimens from Dravuni and Heron I.); 1998: 88 (part, not type specimen).
Lissoclinum verrilli: Monniot & Monniot, 1987: 56.

TYPE LOCALITY. Queensland (Heron I., south reef opposite cay, 8-9m, coll. P.Kott March 1975, holotype QM G9467).

PREVIOUSLY RECORDED. Fiji (Great Astrolabe Group, Dravuni, QM GH59 Kott, 1981). French Polynesia (Monniot & Monniot, 1987).

FURTHER RECORDS. Queensland (Heron I., QM G308346). New South Wales (Jervis Bay, QM G10101).

COLONY. Colonies are soft and grey, with white spicules in the surface and basal layers of test and sometimes more sparsely in the test connectives between them. The anterior part of each zooid is embedded firmly in the surface layer of test. Cloacal canals penetrate between thoraces, and deeper canals surround large clumps of zooids, leaving a single ligament connecting each clump to the basal layer of test. Sometimes spicules appear to encapsulate the ventral surface of the

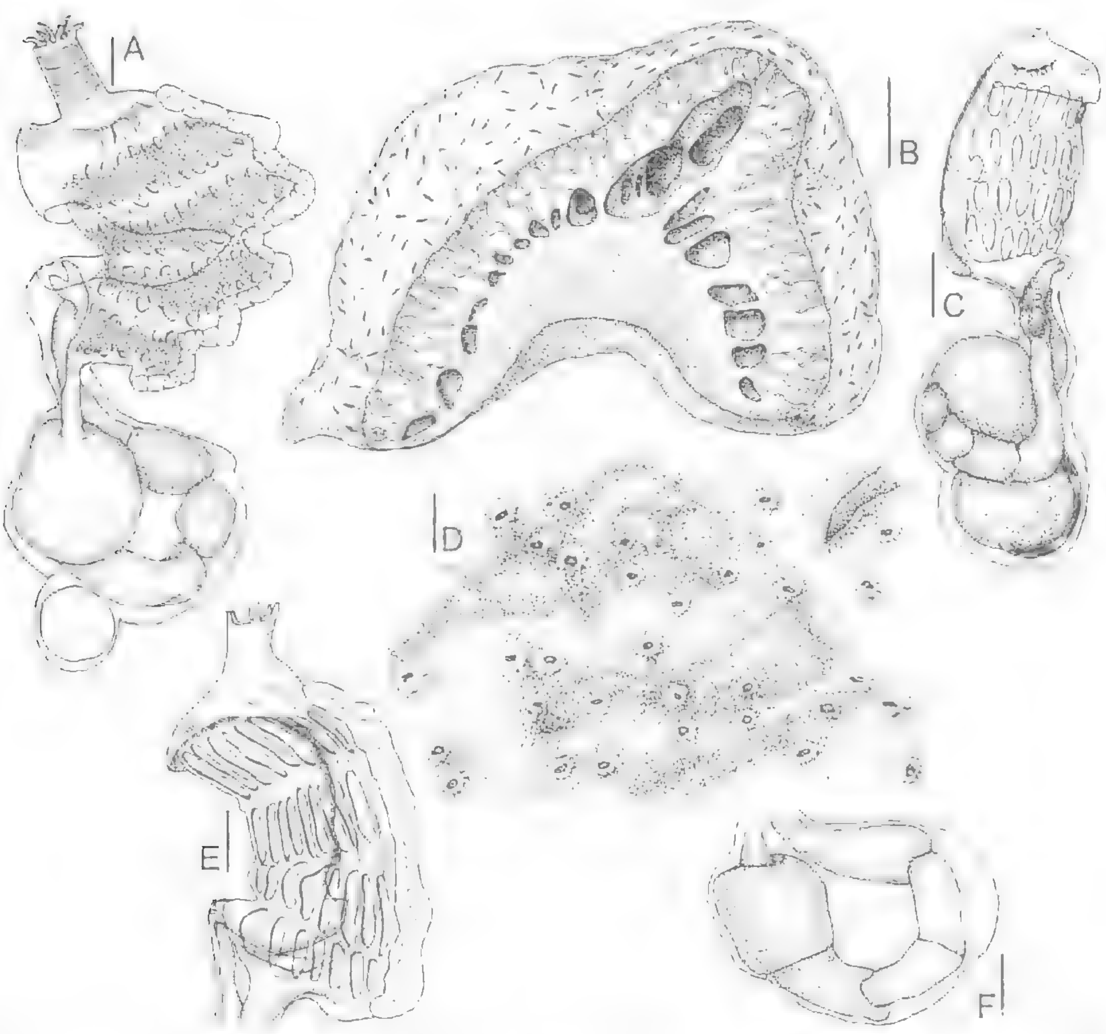


FIG. 146. A, *Lissoclinum sente* sp. nov. (QM G9467) – A, zooid. B,C, *Lissoclinum spongium* sp. nov. (B, QM GH4371; C, QM GH4372) – B, semidiagrammatic vertical section through colony showing slit-like branchial apertures and the position of zooids and common cloacal cavities; C, zooid. D–F, *Lissoclinum tarutara* (QM GH335) – D, surface of a portion of the colony showing branchial apertures in double lines; E, thorax; F, gut loop from ventral surface. Scales: A, 0.1mm; B, 2.0mm; C, E, F, 0.2mm; D, 1.0mm.

thorax, but this is apparent only, the spicules being in the test and only the ventral surface of the thorax is covered by a strand of test.

Spicules have 4–8 long, narrow pointed arms, without a central mass of either free or compacted accessory rays. They measure about 0.08mm from tip to tip of the long arms.

ZOOIDS. Zooids are large, about 1.5mm long, excluding gonads. The cylindrical branchial siphon is muscular, with 6 small pointed petal-like lobes around the rim of the opening. Musculature on the remainder of the zooid is very fine, with a few longitudinal bands in the parietal body wall, and only about 5 fibres in each of the dorsal pharyngeal muscles. The transverse muscle bands between the rows of stigmata have about double that number of fibres. There is no retractor muscle. The stigmata are lined with the thin, flat epithelial cells characteristic of this genus. About 14 stigmata are in each of the rows in the delicate branchial sac. The gut forms a simple almost vertical loop.

A small egg is attached to the posterior side of the gut loop by a narrow ligament. In some

specimens yellow eggs, presumably fertile, are in the test connectives between basal test and surface clumps of zooids, but larvae are not present in any of the newly recorded material. A spherical testis with the vas deferens from its dorsal side is present in the material from French Polynesia, as are larvae. These have a trunk 0.64mm long, with 3 anterior adhesive organs in the anterior mid-line. The tail is wound about halfway around the trunk. Four pairs of lateral ampullae are on each side of the adhesive organs. The sensory vesicle protrudes from the upper surface of the oozooid, about halfway along the trunk. A blastozooid is present.

REMARKS. The long, narrow arms of the spicules resemble those of *L. tasmanense*. They lack accessory rays, either free, needle like ones like those of *L. calycis*, or compacted rays forming a central mass as in *L. verrilli* from Florida and the Gulf of Mexico (see Kott, 1981) and some spicules assigned to *L. tuheiavae* (Monniot & Monniot, 1987, pl. 4B,C). *L. tasmanense* can be distinguished by the large numbers of lateral ampullae in the larvae. *L. pacificense* (Kott, 1981), known only from its holotype and paratype from Fiji, has a larger larval trunk (1.2mm long) than the present species, 6 long stalked globular larval ampullae per side, 2 blastozooids and its spicules have some needle-like spines projecting from the central mass that are not present in *L. semeni*.

Lissoclinum spongium sp. nov.
(Figs 146B,C, 176A)

TYPE LOCALITY. Lord Howe I. (lagoon, sandy reef, depth 1m coll. N.Coleman 23.10.87, holotype QM GH4372, paratypes QM GH4371).

COLONY. Colonies are sessile, domes or irregular, upright masses to 3cm diameter and about 3cm high attached to stalks of weed in crowded populations. One to 5 rather inconspicuous common cloacal openings are on the upper surface, distinguished from the branchial openings by their circular shape and the dark pigment around them. Branchial apertures are simple slits. Zooids are in a thick surface layer around the outside of the whole colony, with the exception of the base. Deep canals surround clumps of zooids and extend into narrow canals that penetrate the test around the thoraces, and into large cloacal cavities beneath the zooid layer that separate the central test core from the outer zooid-containing layer of the colony. The centre and base of the colony is solid zooid-free test, crowded with spicules. Spicules become sparse in the test strands around the zooids, but are crowded again at the surface, at the level of the branchial siphons. Spicules, to 0.025mm in diameter, are all burr-shaped and globular being composed of crowded needle-like radial rays. *Prochloron* is in the common cloacal chambers.

ZOOIDS. Fully expanded zooids are about 1.5mm long, excluding the gonads. The branchial aperture is a transverse slit, with an anterior and a posterior lip. About 6 muscles radiate from each end of the apertures. Muscles in the remainder of the thorax are very delicate. The atrial aperture is wide exposing most of the branchial sac directly to the cloacal cavity. In the isolated zooids, a vertical flap about halfway up each side of the atrial aperture is the lateral organ. The branchial sac has about 6 oval stigmata in each row and small conical dorsal languets between the rows. The gut loop is bent ventrally from the base of the vertical oesophageal neck, the stomach, duodenum, posterior stomach and proximal part of the rectum making a horizontal loop. A large spherical testis is posterior to this horizontal loop, and the vas deferens hooks around it to extend straight to its opening near the anus at the posterior end of the thorax.

REMARKS. Colonies resemble small *Didemnum molle*, but lack the large terminal cloacal aperture, have slit-like branchial apertures, and less extensive cloacal cavities, and do not produce large quantities of mucus as in *D. molle*.

Although it shares many characters (slit-like branchial apertures, spherical spicules, undivided testis, and small colonies) with *L. bistratum* its colonies are much thicker with a central (rather than basal) test mass, and the spicules are smaller than those of *L. bistratum*.

Lissoclinum taratara
Monniot & Monniot, 1987
(Figs 146D–F, 177G)

Lissoclinum taratara Monniot & Monniot, 1987: 52.
Echinoclinum triangulum: Millar, 1975: 241.

NEW RECORD. (Queensland (Lizard I., QM GH 335).

PREVIOUSLY RECORDED. French Polynesia (Monniot & Monniot, 1987) Indonesia (Millar, 1975).

COLONY. The newly recorded colony is soft and fleshy. It has a spicule-free superficial bladder cell layer which sometimes is very thick. Beneath the bladder cell layer, the spicules are not crowded but are fairly evenly distributed, absent only from the base of the colony. Deep circular cloacal canals extend almost the full depth of the

zooids but in the newly recorded specimen there are no posterior abdominal cloacal spaces. Zooids line each side of the canals, their ventral surfaces embedded in the stands of solid test.

Spicules are large, about 0.1mm between tips of the larger tetrahedral rays. Shorter and finer spicule-rays radiate out from the centre of each spicule. There is a deal of variation in the numbers and the length of the spicule rays. The spicules tend to break up. The colony is white in preservative but its colour in life is not known.

ZOOIDS. Zooids are large, the thorax and abdomen together more than 2mm long. The thorax, longer than the abdomen, has a moderately long branchial siphon that penetrates the bladder cell layer. Neither retractor muscle nor atrial tongue are present. The branchial sac has 4 rows of stigmata with about 8 or 9 long stigmata in the anterior 2 rows, and 7 in the posterior row. Longitudinal muscles in the parietal body wall are very conspicuous. The gut loop is rounded but almost vertical with a roomy duodenum, an oval posterior stomach and a pronounced constriction between the proximal and distal parts of the rectum.

Gonads were not present in the newly recorded specimen. In the French Polynesian specimens the testis is undivided and more or less pyramidal, with the vas deferens originating from the apex of the pyramid. Larvae are known for Indonesian material (Millar, 1975). They have a trunk 0.6mm long, with 3 adhesive organs, 4 pairs of lateral ampullae, and they lack blastozooids.

REMARKS. The newly recorded specimen resembles the type material in all aspects of the colony, zooid, and spicules. The species is distinguished from *L. vulgare* Monniot, 1992 from New Caledonia by its larger spicules which have a more conspicuous difference between shorter narrower central rays and thicker, longer tetrahedral arms than in *L. vulgare* (in which all the rays are a similar thickness). The species also lacks the posterior abdominal cloacal cavity of *L. vulgare*. The spicules have fewer and thicker rays than those of *L. calycis*, and the colonies are firmer with a distinct bladder cell layer. *L. pacificense* from Fiji also has some similarities to this species, but its tetrahedral rays are shorter, and the central needle-like rays are shorter, and finer. Spicules of *L. sente* (> *L. verrilli*: Monniot & Monniot, 1987) have no central rays at all, its spicules resembling *L. tasmanense* from southern Australia. *Echinoclinum triangulum*: Millar, 1975, which Kott (1980) erroneously accepted as belonging to *L. triangulum* (Sluiter, 1909), has spicules like those of the present species with which it appears to be conspecific. The present species is distinguished from *L.mereti* Monniot & Monniot, 1987 by its longer, thicker, well separated spicule rays and by the larvae, which are the same size but lack the blastozooids found in *L. mereti* (see *L. triangulum*).

Lissoclinum tasmanense (Kott, 1954)
(Figs 147, 177-I; Pl. 20G,H)

Cystodytes tasmanensis Kott, 1954: 155.
Lissoclinum tasmanense: Kott, 1998: 88.
Echinoclinum verrilli: Kott, 1962: 312; 1972a: 21.

NEW RECORDS. Western Australia (Rockingham, QM G300949; King George Sound, SAM E2688). South Australia (Great Australian Bight, Fowlers Bay, SAM E2640; Topgallant I., QM GH1288, G302149; Point Turton, SAM E2621; Edithburgh, E2626; Coobowie Bay, QM GH2416; Tipara Reef, QM GH3705; Eyre Peninsular, SAM E2608). Tasmania (Maria I., AM Y2320).

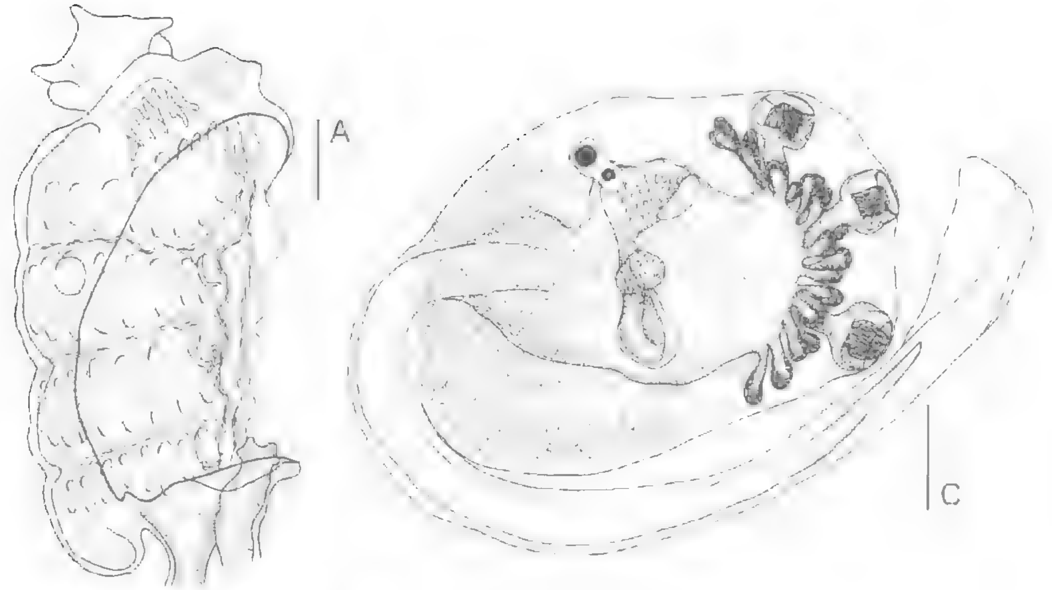
PREVIOUSLY RECORDED. South Australia (Halletts Cove, SAM E2435, E2649 Kott, 1972a). Tasmania (off Maria I., Kott, 1954, 1962).

The species is said to be common in St Vincent Gulf. It is recorded to 174m (Kott, 1954).

COLONY. Living colonies are soft, white and jelly-like, usually disintegrating when removed from the substrate. Spicules form a spiny tough capsule around the thorax and abdomen and sometimes are also scattered through the remainder of the test. They have 6–8 long narrow, smooth pointed arms, and measure up to 0.1mm between the tips of adjacent arms. The capsule of spicules around the abdomen is particularly compact, formed of a single layer of spicules with their arms interdigitating and others projecting hedgehog-like around the abdomen. Embryos are found free in the test, outside the spiny capsule. Zooids are in long double rows each side of canals that are as deep as the full length of the zooid.

ZOOIDS. Zooids are of moderate size about 1mm overall when contracted. They are difficult to remove from the capsule of spicules. A muscular branchial siphon has 6 small pointed lobes around the rim of the aperture. At least 8 stigmata are in each row in the branchial sac, although the zooids are all too contracted for exact counts. A large circular lateral organ is on each side of the thorax. The gut loop is about half the length of the body, and oesophageal buds are present in the same colonies as developing embryos (SAM E2435). The testis is undivided.

Several colonies from South Australia,



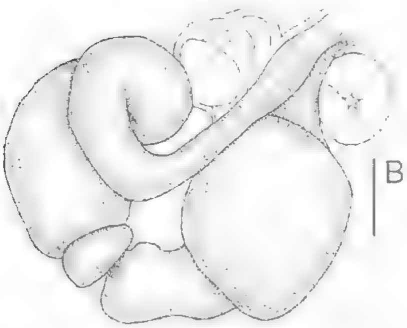


FIG. 147. *Lissoclinum tasmanense* sp. nov. (A,B, SAM E2626; C, SAM E2435) – A, thorax; B, abdomen with oesophageal buds; C, larva with blastozooid, opaque cells at the posterior end of the larval trunk, and terminal columnar cells on the tips of the ectodermal ampullae. Scales: A,B, 0.1mm; C, 0.2mm.

collected in August and December (QM GH2416, SAM E2435) and in March (SAM E2640) have embryos developing in the test. Larvae are large, the trunk about 1mm long, and the tail wound about halfway around it. Three large, stalked adhesive organs, with a wide axial cone in each epidermal cup, are in the anterior mid-line. About 24 (12 per side) balloon-like epidermal ampullae on narrow stalks project from the larval epidermis around the base of the adhesive organs. These have thin epithelial walls except on their terminal surface where longer cells form a cap. The cerebral vesicle, with otolith and ocellus, is in a protuberance over the anterior end of the oozooid. Four rows of about 8 stigmata are in the oozooid and at least one blastozooid is present. It is possible that there is a second, although this is obscured by irregular, comma-shaped, triangular or fusiform opaque bodies crowded in the larval test around the posterior half of the trunk, becoming sparse toward the anterior end. The larval body narrows abruptly behind the oozooid and blastozooids, which are about halfway along the trunk.

REMARKS. The long smooth arms of the spicules are different from most others in this genus except *L. sente* (> *L. verrilli*: Monniot & Monniot, 1987), which has smaller larvae with fewer (only 4 pairs) lateral ampullae, although these are similar to the balloon-like ones of the present species. *L. pacificense* (Kott, 1981), from Fiji, also has large larvae, but 6 balloon-shaped lateral ampullae are on each side and spicules have a tuft of short spiky needle-like spicule rays in the centre.

Similar opaque bodies in the larval test to those in the present species have been observed in other species of *Lissoclinum* (see genus *Lissoclinum* above). Sometimes these are absent only from windows over the sense organs, and in front of the adhesive organs. In the present species they are crowded in the posterior half of the trunk.

Lissoclinum timorense (Sluiter, 1909)
(Figs 148A,B, 178C–E)

Didemnum timorensis Sluiter, 1909: 51.
Lissoclinum timorense: Kott, 1998: 88.
Didemnum voeltzkowi Michaelsen, 1920: 54 (part, syntypes ZMH K1099). Hastings, 1931: 97.
Lissoclinum voeltzkowi: Kott, 1980: 13; 1981: 190; 1982a: 112. Ryland et al., 1984: 272. Monniot & Monniot, 1996: 175.
Lissoclinum bistratum: Monniot, 1992: 566.

NEW RECORDS. Queensland (Heron I., QM G12633; Lizard I., QM GH158). West Pacific (Solomon Is, USNM 18353). Western Pacific (Palau Is, QM GH911)

PREVIOUSLY RECORDED. Queensland (Low Is – BMNH 30.12.17.43-44, AM Hastings 1931; Heron I., Green I., Lizard I. – QM G9913, G12621 Kott, 1980; 1982a). Indonesia (paralectotype ZMA TU482, lectotype TU1274 *D. timorensis* Sluiter, 1909). West Pacific (New Caledonia – Monniot, 1992; Caroline Is, Philippines, Palau Is – Kott, 1982a, Monniot & Monniot, 1996; Guam – QM GH827 Kott, 1982a; Fiji – Kott, 1980, 1981). West Indian Ocean (Malagasy – syntypes ZMH K1099 *L. voeltzkowi* Michaelsen, 1920).

Kott (1980) proposed that habitat requirements of this species are more stringent than for other *Prochloron*-ascidian symbioses. Vast populations are found near the low tide mark on the outer part of the open, sandy reef flat at most Fijian locations. These populations are crowded, the borders of the polygonal colonies contiguous, forming a close mosaic. At Lizard I. similar populations were found on driftwood (Kott, 1982a), but not on the reef flat. At this location *L. bistratum* occupies similar reef flat habitats as the present species does in Fiji. Populations at Green I. were on brown weed on the inner reef flat, and did not form such close mosaics as those directly on the sandy surface of the reef at Fijian locations. Only a few records of this species are from Heron I. and it is possible that the species cannot accommodate the diurnal changes on the reef flat at this southerly location.

COLONY. Colonies are up to 0.5cm thick and sometimes form large sheets to about 9cm in maximum dimension (Sluiter, 1909; Kott, 1982a) or, when found in crowded populations, small flat-topped cushions, to 4cm in greatest dimension, polygonal, with straight edges, forming a close mosaic with adjacent colonies. In less crowded populations the colony outline is more oval. Colonies appear to subdivide to form these crowded populations. In life they are dirty greyish-brown, or cream, or greenish-cream, depending on the concentration of spicules in the surface. Crowded brown-black spherical pigment cells are scattered in the surface, and are concentrated in small evenly-spaced patches, alternating with the branchial apertures around the upper surface of each colony, just inside the rounded outer margin which is produced into pointed spicule filled papillae, one outside each branchial aperture. Similar papillae sometimes occur on other parts of the upper surface. Newly recorded specimens from the West Pacific (USNM 18353) contain a mixture of larger sheets and small oval colonies, both with characteristic papillae around the outside of the colony. Colonies are only loosely attached to the substrate. One or 2 common cloacal apertures are on short chimneys projecting from the upper surface with pigment cells crowded around them. Branchial apertures are transverse slits. Green *Prochloron* in the cloacal cavity can be seen through branchial apertures in the living colonies.

Spicules are crowded around the outside and in the base of the colony. They also are crowded in the surface test when the colonies are exposed, but in shaded habitats the spicules in the surface test are less crowded and green *Prochloron* in the cloacal cavity can be seen through the surface test. Spicules are absent from the area around the cloacal apertures. The spicules are stellate to 0.04mm in diameter with 7–9 conical rays in optical transverse section, the conical rays set in polygonal bases; or with chunky club-shaped, sometimes flat-tipped rays (the same number or more numerous than in the stellate spicules). Both the conical tip and the polygonal base of the stellate spicules vary in length from spicule to spicule. These two type of spicules are present in different proportions, sometimes those with club-shaped rays being more numerous and in other specimens those with octagonal bases and conical tipped rays predominating. Occasionally some globular spicules occur, but always these are rare.

The common cloacal cavity is 3-dimensional, with secondary canals at thoracic level and very extensive posterior abdominal chambers which appear to divide the colony into 2 horizontal layers. In the living colonies, these spaces are kept inflated by pressure of the excurrent water, raising the surface test.

ZOOIDS. Zooids are about 0.8mm long. Branchial apertures are transverse slits with dorsal and ventral rounded lips. The atrial aperture is wide, exposing most of the branchial sac directly to the exterior. Tapering columnar epithelial cells project from the anterior part of the thorax. Eight long, oval stigmata are in each row in the branchial sac . An oval lateral organ is opposite the third row of stigmata. A projecting retractor muscle is not present. The gut loop is short and horizontal, bending ventrally from the oesophageal neck. The testis is undivided and

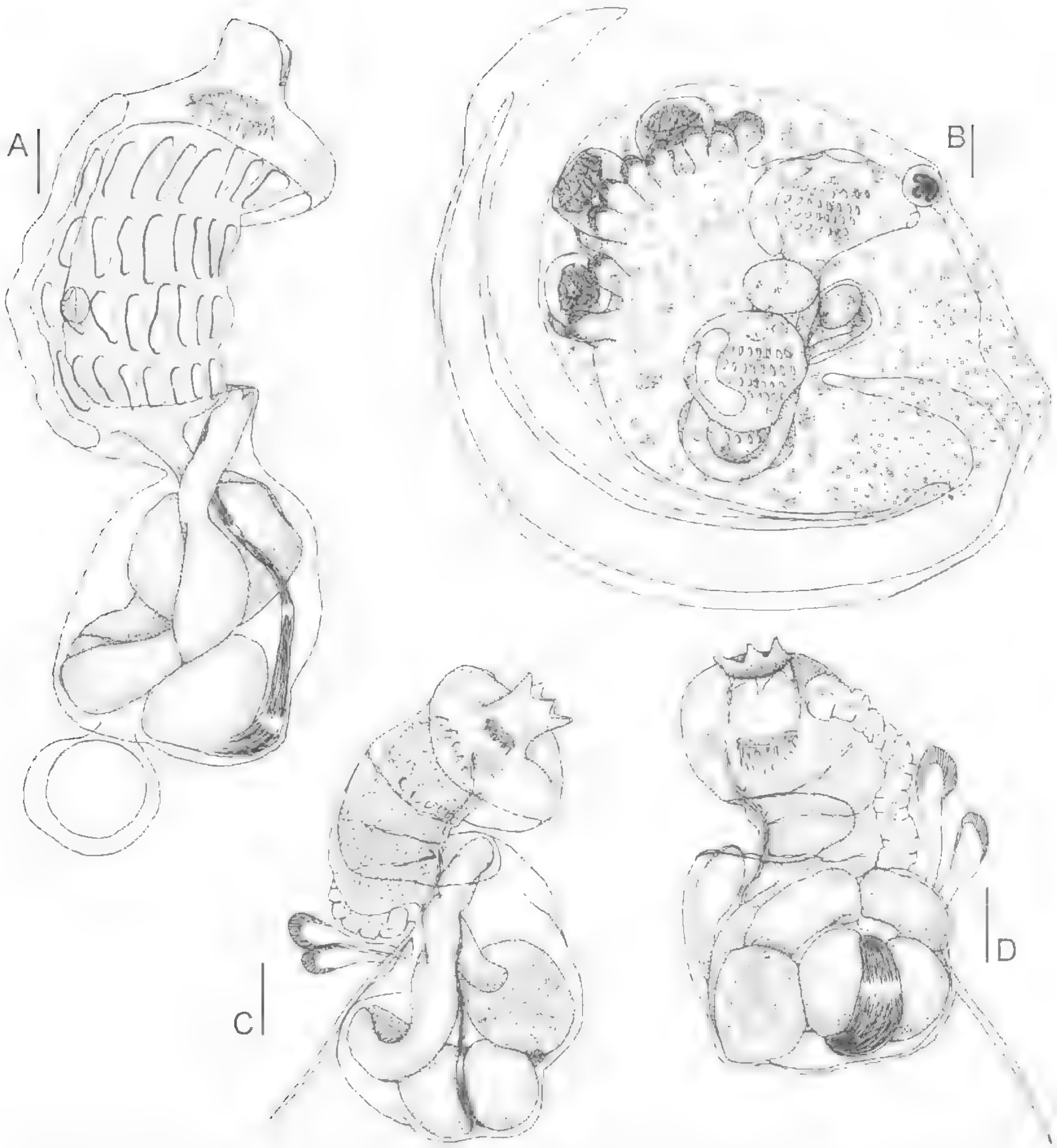


FIG. 148. A, B, *Lissoclinum timorense* (ZMA TU482) – A, zooid; B, larva showing thoracic and abdominal buds of blastozooid, terminal columnar cells on tips of ectodermal ampullae, opaque cells in larval test, and *Prochloron* adhering to the test around the posterior end of the larval trunk. C, D, *Lissoclinum variabile* sp. nov. (QM G308008) – C,D, zooids from left and right sides, respectively. Scales: 0.1mm.

projects posteriorly back from behind the flexed distal part of the gut loop. The vas deferens is hooked around the posterior end of the testis follicle, extending up along its dorsal border to the atrial cavity.

Embryos are in specimens from Green I. in August, Lizard I. in June (QM G9913, G12621) and Fiji in July. Larvae are large, the trunk 1.5mm long and the short tail wound about halfway around it. Three large antero-median adhesive organs, have 8 lateral ampullae along each side. The epithelium along the free anterior end of each ampulla is differentiated into columnar, possibly adhesive, cells. An oozooid and 2 blastozooids are about halfway along the trunk, each with 4 rows of stigmata. *Prochloron* cells form a cap

around the narrow pointed posterior end of the larval trunk and the test in front of this cap appears to be growing back to enclose *Prochloron* cells in what is probably the developing cloacal cavity.

REMARKS.The close relationship and distinguishing features between this species and *L. bistratum* are discussed under that species above.

Lissoclinum timorense (Sluiter, 1909) from Indonesia was described from a single specimen (broken into two specimen lots, ZMA TU1274 and ZMA TU482). It is a thin, hard, sheet (like colonies from the Palau Is, see Kott, 1982a) with spicules crowded everywhere except in the superficial layer of test at the level of the branchial siphons, where patches occur only occasionally. Spicules are up to 0.06mm in diameter, some have up to 15 club-shaped blunt-tipped rays, but others have only about 7 polygonal bases in optical transverse section with conical tips of various lengths set in them. The extensive, horizontal posterior abdominal cloacal cavity is crowded with *Prochloron*. Although Sluiter (1909) referred to a likeness to *L. bistratum* he did not observe the symbionts which, even in the long-preserved holotype pour out of the cloacal cavity in thick clouds when it is cut. Although (Sluiter, 1909) reported a coiled vas deferens, this was not found on re-examination of the types. Some large embryos with an almost spherical trunk, 1.0mm long, 8 rudimentary ampullae and the tail wound completely around it, are in the holotype.

Syntypes of *Didemnum voeltzkowi* Michaelsen, 1920 from Madagascar (ZMH K1099) are 4 narrow colonies to about 2cm long. They have characteristic zooids, and surface papillae are associated with some (but not all) of the bilobed branchial apertures around the margins of the colony. Spicules are predominately club-shaped but some have characteristic polygonal bases with pointed conical tips. The Cloacal cavities are packed with *Prochloron*. Zooids are small with 7–8 stigmata per row, and lack a retractor muscle. Other colonies (ZMH K1111) from Malagasy assigned to this species by Michaelsen (1920) belong to *L. bistratum*.

Specimens from the Palau Is, questionably assigned to this species by Monniot & Monniot (1996: 176), are said to have spicules 'not exactly similar to those of either *L. voeltzkowi* or *L. bistratum*'. These spicules have neither been figured nor described, nevertheless it is possible to assign these specimens to the present species as spicules of *L. bistratum* are uniform while those of *L. timorense* are variable and diverse and the specimens have brown pigment (without red or yellow carotenoids), 8 stigmata per anterior row in the branchial sac and papillae on the surface of the colonies.

Projecting columnar cells on anterior parts of the thorax occur also in *L. nebulosum* and *L. variabile* and in most *Didemnum* and *Polysyncraton*, although their occurrence does not imply a phylogenetic relationship. Some spicules of the present species resemble those of *Didemnum digestum* and *D. uturoa*, but the occasional large rays of those 2 species do not occur.

The small lobulating colonies that form a mosaic over the Fijian reef flats and that occur at Green I. and Lizard I. are identical in every way to the sheet-like ones, except in their colony size and growth habit. Possibly lobulation is a direct response to crowding.

Lissoclinum triangulum (Sluiter, 1909) (Fig. 177A)

Diplosomoides triangulum Sluiter, 1909: 86.
Lissoclinum triangulum: Kott, 1977: 620; 1998: 89.
Echinoclinum triangulum: Kott, 1980: 21.
Not *Echinoclinum triangulum*: Millar, 1975: 241 (< *L. taratara*).
Echinoclinum philippinensis Tokioka, 1967: 93.

NEW RECORDS. Queensland (Heron I., QM GH1345, GH2266; Green I., QM GH430; Lizard I., QM GH112, GH123).

PREVIOUSLY RECORDED. Queensland (Heron I. –QM GH12623 Kott, 1977, 1980). Indonesia (Sluiter, 1909). Philippines (USNM 11790-1 Tokioka, 1967).

The species is found in cryptic habitats in rubble zones and below low tide levels to 20m around coral reefs.

COLONY. Colonies are soft and flat up to 6cm in maximum extent and up to 0.5cm thick. Bladder cells are present throughout the test. Spicules are in a layer beneath the superficial layer of test, and they form a capsule around each zooid. They become sparse, and in smaller specimens are absent, toward the base of the colony. Also in smaller specimens, the capsule of spicules around the zooids is particularly thin.

Spicules are flattened with fine needle-like rays of different sizes — small on each side and longer around the edges where they determine the diamond or triangular outline of each spicule by progressively lengthening toward the points. Spicules are up to 0.08mm in greatest dimension.

The cloacal cavity is 3-dimensional with deep canals around each clump of zooids. These deep

canals extend into posterior abdominal spaces. The latter are interrupted by connectives joining each clump of zooids to the basal test. Secondary thoracic cloacal cavities penetrate amongst the zooids in each clump. Plant cells are present in the cloacal cavity and embedded in the test. Their identity is not known.

ZOOIDS. Zooids are relatively large, about 1.5mm long, despite the abdomen usually being bent up across the posterior end of the thorax. The branchial aperture has 6 distinct pointed lobes. The atrial aperture is wide exposing most of the branchial sac directly to the common cloaca. About 12 long, narrow stigmata are in each row of the branchial sac. A narrow lateral organ is about halfway up the thorax on each side of the endostyle. A retractor muscle is not present. The gut forms a simple loop with the proximal part of the rectum flexed up over the gonads. A straight vas deferens extends from the dorsum of an undivided testis.

Larvae have not been recorded from Australian specimens. In discussing *L. mereti*, Monniot & Monniot (1987:50) described the larvae from the type specimen of the present species as having a trunk 1.2mm long, and 6 pairs of ectodermal ampullae. Blastozooids were not detected.

REMARKS. Millar (1975) assigned specimens from Banda, Kei I. and Amboina (*L. triangulum*: Millar, 1975) to this species. However, the spicules of Millar's specimens appear to be more like those of *L. taratara* with large, thick, separated rays. Further, although the larvae Millar (1975) described, lack blastozooids, they have a trunk only 0.6mm long with 4 pairs of lateral ampullae like *L. mereti*, which however does have larval blastozooids and spicules different from Millar's specimens. *L. mereti* has spicules like the present species and differs from it principally in its larval blastozooids and fewer lateral ampullae.

Kott (1980) examined the syntypes of *E. philippinensis* Tokioka, 1967 (USNM 11790-1) and assigned them to the present species, as Millar (1975) had suggested — albeit they are not conspecific with the specimens Millar had before him (< *L. taratara*).

Lissoclinum variabile sp. nov.
(Figs 2C, 148C,D, 178F)

DISTRIBUTION. TYPE LOCALITY. Queensland (Heron I., eastern end of reef, low tide, coll. P. Kott 9.3.93, holotype QM G308008).

COLONY. The colony is soft, gelatinous and appears to be black in life owing to the black zooids seen through the transparent test. The colony is very delicate with a huge cloacal cavity. Zooids are in separate branches of the narrow test strands that connect the thin surface and basal layers of test.

Spicules are never crowded, but they are evenly distributed throughout the test. They are particularly diverse, and include stellate spicules with up to 17 short conical rays in optical transverse section, and others with as few as 5 longer, more acutely pointed rays in optical transverse section. Spicules with more or less flattened tongue-shaped rays and globular spicules with crowded flat-tipped rays also occur. Spicules are mostly about 0.03mm diameter, but larger ones to 0.09mm diameter are scattered amongst them.

ZOOIDS. Zooids are small, to 0.7mm long, although the distal tip of the gut loop is flexed ventrally. Some columnar epithelial cells project from around the base of the branchial siphon. Brownish-black squamous epithelium persists in the body wall over the stomach and the rest of the gut loop. The thorax is long with 4 rows of about 8 rather long rectangular stigmata per row. The large atrial aperture exposes most of the branchial sac directly to the cloacal cavity. Fine muscles are in the transverse vessels, and dorsal pharyngeal muscles continue in the long retractor muscle extending posterior to the abdomen. The divisions of the gut loop (other than the spherical stomach) are inconspicuous. The testis lies behind the flexed distal part of the gut loop. It is divided into 2 follicles and the vas deferens extends anteriorly between them, short vasa efferentia issuing from their distal ends. Two vascular appendages extend from the ventral concave part of the gut loop. They extend away from the zooid in the test connectives and are conspicuous principally because of their terminal ampullae.

REMARKS. Black squamous ectoderm surrounding the abdomen is conspicuous both in living and preserved zooids, and is clearly seen through the transparent test, as in *Diplosoma listerianum*. *D. listerianum* also has a retractor muscle and 2 testis follicles but lacks spicules. The dark squamous epithelium is present over the abdomen in *Didemnum albopunctatum* and *Polysyncraton orbiculum* as well as over the whole zooid in *Diplosoma* spp. and *Trididemnum* spp. A phylogenetic relationship is not implied.

L. ravarava Monniot & Monniot, 1987 from French Polynesia and *L. limosum* have similar soft colonies, although their spicules are smaller and less diverse than in the present species, they lack the black squamous epithelium in the body wall, their testes are undivided and they lack retractor muscles. *L. polyorchis* Monniot, 1992, like the present species, has some spicules with flattened rays like those of *Polysyncraton pontoniae*, but it has more numerous testis follicles, lacks a retractor muscle, lacks the diversity of spicules of the present species and has spicules crowded around the margins of the colony. *L. concavum* from southern Australia has similar spicules to the present species, differing in having more male follicles (6) and and in lacking black squamous ectoderm.

Genus **Clitella** gen. nov.

TYPE SPECIES. *Clitella nutricula* sp. nov.

Zooids are arranged in circular systems of up to about 10 around a central common cloacal cavity and aperture . A layer of small spicules encapsulates the abdomen of some of the zooids. Zooids have 4 rows of stigmata, a wide and sessile atrial aperture exposing most of the branchial sac directly to the cloacal cavity, a strong tapering retractor muscle, stronger longitudinal parietal thoracic muscles than in most other genera of the Didemnidae, especially wide dorsal pharyngeal muscles, a long gut loop divided into duodenum, oval posterior stomach (in the loop of the gut), and the proximal part of the ascending loop distinctly separated from the distal part as a prerectal chamber. The testis is undivided. The proximal part of the vas deferens is much expanded into a large seminal vesicle. Larvae are large and produce numerous premature buds in the larval trunk, resulting in up to 7 whole blastozooids (both thoracic and abdominal buds), each successively producing the next blastozooid in the series. The larval trunk is, accordingly, of unusually great diameter, and is an antero-posteriorly flattened thick disc. The tail, from the centre of the posterior surface, winds around the disc in a median groove that separates a shallow right from a left frontal lobe. Each adhesive organ is a convoluted groove on each frontal lobe. Small larval epidermal vesicles (rather than club- or finger-shaped ampullae) are in rows along each side of the adhesive grooves. Conical adhesive organs in an epidermal cup known in other didemnid genera do not occur. The cerebral vesicle is in a sac constricted off from the rest of the trunk.

Thus, although zooids are similar to some *Lissoclinum* spp., the genus is distinguished by the small, separate circular cloacal systems, strong thoracic musculature, distinct retractor muscle, undivided testis, vas deferens expanded into a seminal vesicle in its proximal part and unusual disc shaped larva with very numerous blastozooids, highly modified adhesive organs in the form of convoluted grooves and the cerebral vesicle projecting away above the oozooid and constricted off from it.

The homology of the adhesive grooves with the separate stalked epidermal cups with central adhesive cones of the adhesive organs of other didemnid genera can be seen if a cross section of the groove is examined. The central ridge appears to be homologous with the adhesive cones of all other genera, while the walls of the concavity appear to be homologous with the epidermal cup surrounding the cones. The adhesive grooves of the present genus appear to be the result of extensive lengthening of both the adhesive cones and their epidermal cups into long convoluted tracts. The adaptive value of such a lengthening may be associated with the flattened disc-shape of the larval trunk. While the 3 point adhesion at the narrow end is adequate for the usual didemnid larvae with an oval trunk, adhesion over a wider area may be more effective when the frontal end of the trunk is more or less flattened and the whole trunk is disc-shaped to accommodate the precocious blastozooid production in this new genus.

The budding process also seems to be unusual, in that instead of separate thoracic and abdominal buds being produced always from the oesophagus of the oozooid, each successive blastozooid forms the new blastozooid in the series. The budding process is characteristic of this family, occurring by division across the oesophageal region, leaving the parental thorax with the new abdominal bud and the parental abdomen with the new thoracic bud. The resultant circle of zooids presumably forms the initial system of the colony, its components being in place before settlement and metamorphosis. The atrial apertures are all directed back to the posterior (upper) side of the disc where the common cloaca will be formed as the tail is withdrawn for absorption into the haemocoel of the larval trunk. The best developed blastozooids are those nearest to the oozooid, although in all the gut loop is well-formed and 4 rows of stigmata are present.

A single species, represented only by its holotype, is the basis for the present genus. Its evolutionary distance from *Lissoclinum* is attested by the prolific precocious budding from successive blastozooids and by its unique larval adhesive organs.

The genus name derives from *Clitella* (f.), a pair of panniers or a pack saddle, reflected in the two frontal lobes of the antero-posteriorly flattened larval trunk.

Clitella nutricula sp. nov.
(Figs 2B, 149,150)

TYPE LOCALITY. South Australia (Sir Joseph Banks Group, Marum I. N. Point, reef, rubble sand and sparse *Posidonia* 5-8m, coll. K. Gowlett Holmes and N. Holmes 19.1.86, holotype SAM E2678).

COLONY. The colony is a soft, gelatinous cushion, with a smooth more or less rounded upper surface, rounded margin and a shallow basal concavity where it was fixed over a rounded substrate. It is about 2cm long, 1cm wide and 0.5cm thick. Although soft, the test is resilient and does not tear easily, and zooids are tightly embedded and difficult to remove. It is brownish and translucent, and zooids are a darker brown and show through the test. They are arranged in separate circular systems (about 4mm in diameter) of up to 10 zooids around a simple circular cloacal cavity (at thoracic level) with a central sessile common cloacal aperture. The branchial openings are inconspicuous on the surface and have soft test pulled down into the siphons, which, in these colonies, are also contracted down into the surface. Spicules to 0.04mm diameter are stellate with up to 7 conical rays in optical section, or burr-like with needle-like rays. They form a capsule around the abdomina in some parts of the colony, but are absent completely from other parts. These spicules break up easily if attempts are made to tear the resilient test that contains them.

ZOOIDS. Zooids are much contracted in the holotype colony, thoraces being only about 0.7mm long, and the abdomina about 1mm. Stalked, spatulate-tipped columnar epithelial cells project from the body wall of both the thorax and abdomen (see Glossary, epidermis; Fig. 2B). The thorax is robust, with a well formed branchial siphon, 6 distinct lobes around the aperture and numerous longitudinal muscles that are deflected around the open atrial aperture which exposes most of the middle part of the branchial sac directly to the cloacal cavity. An atrial lip is not present. Dorsal pharyngeal muscles are wide and a strong retractor muscle projects from the posterior end of the thorax. About 14 stigmata are in each row of the branchial sac, although these could not be counted accurately because of contraction. The gut loop is long and vertical with a relatively long

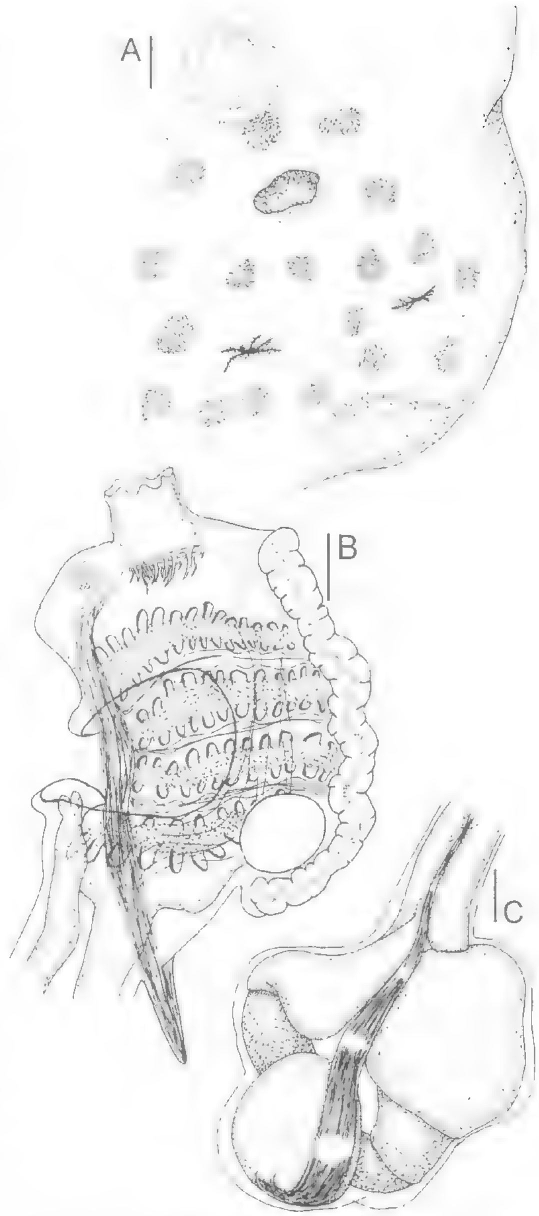


FIG. 149. *Clitella nutricula* gen. nov., sp. nov. (SAM E2678); A, upper surface of part of colony zooids visible through translucent test, larvae just beneath surface; B, thorax; C, abdomen, the proximal part of the vas deferens expanded into a seminal vesicle. Scales: A, 1.0mm; B, C, 0.1mm.

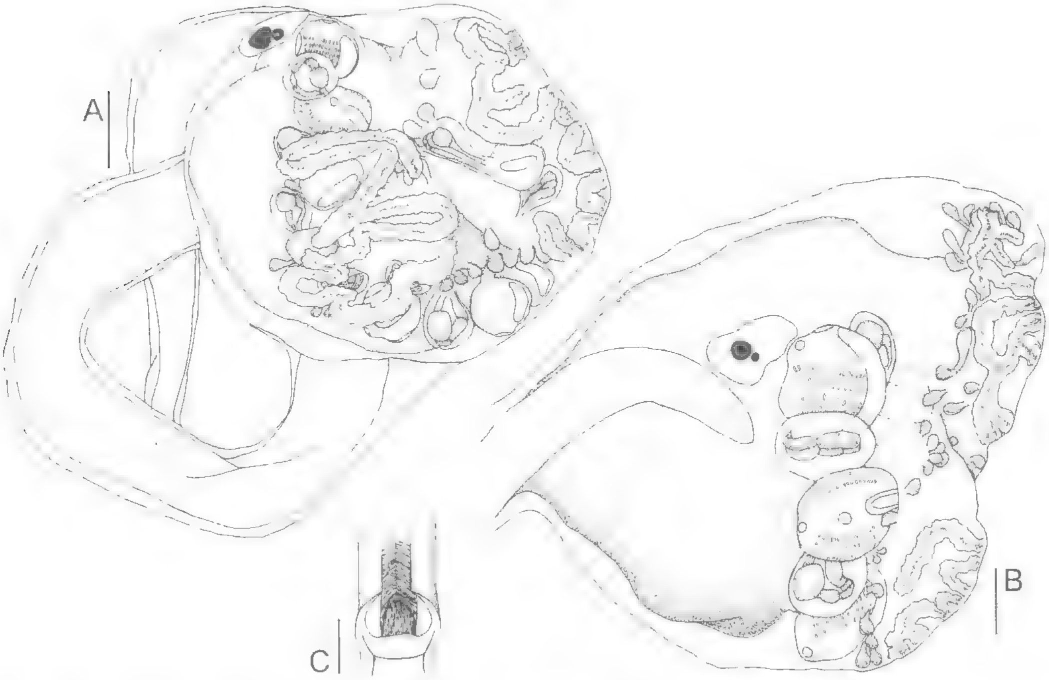


FIG. 150. *Clitella nutricula* gen. nov., sp. nov. (SAM E2678); A, larva from anterior end of trunk showing adhesive grooves, oozooids and blastozooids, ectodermal vesicles; B, larval trunk from above showing oozooid and blastozooids on right side, ectodermal vesicles, adhesive grooves, and the groove in the antero-median line where the tail winds around the trunk; C, diagrammatic section through the end of the adhesive groove (homologous with the epidermal cup of standard adhesive organs) with the continuous ridge of adhesive cells (homologous with the adhesive cone of standard adhesive organs) arising from the base of the groove. Scales: A,B, 0.2mm; C, 0.05mm.

stomach, duodenum and oval posterior stomach in the pole of the loop. The proximal part of the ascending limb consists of a distinct prerectal chamber that is sharply cut off from the narrower distal part of the rectum. The testis is almost spherical and the vas deferens originates from its posterior end as a narrow tube which curves to the right before expanding into a wide seminal vesicle passing over the testes or slightly to its right as it extends anteriorly to the atrial aperture.

The large antero-posteriorly flattened disc-like larval trunk, 2mm in diameter and 1mm thick, has left and right frontal prominences with the convoluted, probably adhesive, groove winding over its surface and small spherical ectodermal vesicles as described above. The 7 whole blastozooids encircle the front of the larval trunk from the oozooid (to the right of the tail) in an anticlockwise direction (frontal view) around the meridian of the disc, in a continuous series with the oozooid. The sensory vesicle projects back and out from the oozooid in a long comma-shaped sac constricted at its base. The oozooid and then each successive blastozoooid produce a thoracic and an abdominal bud, and then divide across the oesophageal region to produce the next blastozooid in the series in the process of oesophageal budding that is characteristic of the Didemnidae. Both oozooid and blastozooids have well-formed adult organs including 4 rows of stigmata and an entire gut loop with its distinct sub-divisions.

REMARKS. *Lissoclinum* spp. with similar distribution of spicules (encasing the abdomina) are in the *verrilli*, *triangulum* and *punctatum* groups. However, the larva has unique adhesive grooves and precocious blastozooids and the colony has simple circular systems of relatively few zooids unusual in the Didemnidae. These characters readily distinguish the species from all others in related *Lissoclinum*. Zooids are less distinctive although they are more muscular than those of *Lissoclinum*, in particular the dorsal pharyngeal muscles are wide, whereas in *Lissoclinum* they are characteristically narrow.

Genus **Diplosoma** MacDonald, 1859

TYPE SPECIES. *Diplosoma rayneri* MacDonald, 1859 (< *Leptoclinum listerianum* Milne Edwards, 1841).

The genus is characterised by its relatively large thoraces, each with a wide open atrial aperture exposing most of the branchial sac directly to the cloacal cavity, a straight vas deferens, testis either undivided or consisting of 2 follicles, and the virtual absence of spicules (some minute ones sometimes are present). Larvae, relatively large and yolky usually having a trunk 0.5–1.0mm or more, are unique in always having an oozooid and one to 3 blastozooids usually at the anterior end of the trunk, often projecting from it and associated with the frontal adhesive array — rather than being in the centre of the trunk and posterior to the yolk mass as they usually are in all other didemnid genera. Four rows of stigmata are in the larval pharynx of both oozooid and blastozooids. As larvae mature the trunk divides horizontally isolating the oozooid from the blastozooids and the adhesive organs.

Zooids in *D. ferrugeum* and *D. listerianum* have large leaf-like branchial lobes that alternate with smaller intermediate ones. *D. translucidum* and *D. velatum* have narrow tentacle-like branchial lobes from a short wide base. They never have an atrial tongue. A retractor muscle is present. The cloacal cavity usually is extensive, being either horizontal with spaces at thoracic level and abdomina embedded in the basal test; or 3-dimensional with thoracic and posterior abdominal spaces, the latter traversed by connectives between basal test and the zooid-containing test of the upper half of the colony; or vast horizontal spaces with zooids entirely embedded in connectives between thin surface and basal layers of test. Abdomina usually are bent ventrally and slightly to the right of the posterior end of the thorax. Often a black pigment spot is present in the body wall near the neural ganglion. This spot is made up of irregular pigment particles in the antero-median rim of the atrial aperture, and although close to the neural ganglion (owing to the withdrawal of the rim of the atrial opening) it is not actually associated with it.

In many species the ectoderm of the abdomen and sometimes also the thorax is black squamous epithelium, seen as a mosaic of black polygonal cells each with a light-coloured nucleus. This epithelium occurs commonly in *Trididemnum* (*savignii* group) but it is also in *Didemnum* (*D. albopunctatum*), *Polysyncraton* (*P. orbiculum*) and *Lissoclinum* (*L. variabile*). Despite this there are few characters shared by *Diplosoma* and either *Trididemnum* or *Polysyncraton* or *Didemnum*. *Diplosoma* most closely resembles *Lissoclinum* in its vast cloacal spaces, large thoraces, large capacious gut, undivided or 2-lobed testis, straight vas deferens, and 4 rows of stigmata in the oozooid. *Diplosoma* differs from *Lissoclinum* in lacking spicules and an atrial tongue and the presence of an oozooid and abdominal and thoracic buds of 1–3 larval blastozooids (often one, or occasionally 2 in *Lissoclinum* and *Polysyncraton*, and sometimes one in *Didemnum*) at the anterior end of the larval trunk (anterior to the yolk mass).

The replication rate of certain species in this genus, and consequently their growth rate, is high, often 4 or more generations of replicates being formed simultaneously in the oesophageal region (Kott, 1980). Consequently the 2-dimensional colony growth (a property of Didemnidae generally) may proceed at a greater rate than in other genera, resulting in very thin colonies spread over vast areas (*D. simile*, *D. listerianum*). Colony replication probably also occurs in some species (e.g. *D. virens*: Ryland et al., 1984), reflecting an additional aspect of the growth process.

Obligate symbioses of certain tropical *Diplosoma* spp. with the prokaryotic *Prochloron* occur. Although their biomass is considerable, the number of species involved — *D. multipapillatum* Kott, 1980, *D. simile* (Sluiter, 1909), *D. virens* (Hartmeyer, 1909) — is not as great as in *Trididemnum* or *Lissoclinum*. *D. simile* and (to a lesser extent) *D. virens* are conspicuous in coral reef communities and may cover greater areas in the tropics than any other species in any genus. The species of *Diplosoma* in obligate symbiosis with *Prochloron* always have the plant cells in the common cloacal cavity rather than in the test. All these species have a distinctive organ (the rastrum) by which the algal cells are transferred from one generation of the host species to the next (Kott, 1980; 1981; 1982a,b). The larval test over the rastrum is broken up into a brush of hairs which gather and enmesh plant cells as the larva, having been incubated in the basal test of the colony, breaks into the common cloacal cavity through the layer of plant cells that line it. Although in other genera, parts of the larval test over the trunk (*Lissoclinum* spp. and *Didemnum* spp.) and even the whole test (*Trididemnum* spp.), incorporate symbiotic cells before release from the parent colony, it is only in *Diplosoma* that this special organ has evolved for the

purpose. Monniot (1993) referred to a concavity beneath the larval tail of *Polysyncraton multipapillae* as a rastrum. This is an incorrect use of this term (see Glossary).

Diplosoma is the least diverse genus known in this family. This may result partly from difficulties in distinguishing species from one another owing to an impressive uniformity in the appearance of both colony and zooids after fixation and preservation. This post-mortem resemblance relates to most known species (with the exception of the *Prochloron* symbioses). Rowe (1966) synonymised *D. listerianum* Milne Edwards, 1841, well known in European waters, with *D. macdonaldi* (Herdman, 1886) from the tropical Atlantic (Brazil) and the western Pacific (Gottschaldt, 1898; Van Name, 1918), and *D. mitsukurii* (Oka, 1892) from Japan. Although these specimens look very similar in preservative, their appearance in life may be different and additional information on aspects of their morphology and biology could reflect their genetic distinctness. At present, however, *D. listerianum* appears to be a truly cosmopolitan species being recorded in tropical and temperate waters of all oceans.

The few species in this genus represented in Australian waters are relatively common. The tropical *Prochloron/Diplosoma* symbioses are common and well documented and, although less well known, there also are several non-symbiotic tropical and temperate species, both cosmopolitan and indigenous.

KEY TO THE SPECIES OF *DIPLOSOMA* RECORDED FROM AUSTRALIA

1. *Prochloron* in common cloacal cavity 2
   Prochloron not in common cloacal cavity 3
2. Retractor muscle free from posterior end of thorax . . . . *D. simile*
   Retractor muscle free from halfway down oesophageal neck . . . . *D. virens*
3. Stigmata 8–10 per row; without opaque morulae in test. . 4
   Stigmata 10–12 per row; with opaque morulae in surface, basal and connecting strands of test. . . . . *D. ferrugeum* sp. nov.
4. Black point usually in mid-dorsal body wall near nerve ganglion; larval tail winds three-quarters of the way around the trunk . . . . *D. listerianum*
   Black point never in mid-dorsal body wall near nerve ganglion; larval tail reaches only to anterior end of trunk 5
5. Test tough; groups of zooids attached to floor of common cloacal cavity by short unbranched or slightly branched test connectives . . . . *D. translucidum*
   Test not tough; groups of zooids attached to floor of common cloacal cavity by long branched test connectives . . . . *D. velatum* sp. nov.

The following species are recorded from the western Pacific but not from Australia:

Diplosoma ata Monniot & Monniot, 1987, from French Polynesia and New Caledonia (Monniot, 1994) has a thin beige/white sheet-like colony with black squamous epithelium around the branchial siphon, endostyle and gut, and a black spot near the cerebral ganglion. Its testis is undivided and its larva has 3 pairs of lateral ampullae in a trunk 0.55mm long. A short retractor muscle projects from the posterior end of the thorax in some zooids, although in others there is a circum-oesophageal annulus (probably a muscle) but no retractor (see Monniot & Monniot, 1987). The cloacal cavity in this species has not been described. The zooid figured by Monniot & Monniot (1987, fig. 20A) was presumably taken from the holotype. Zooids of *D. ata*: Monniot, 1994 appear to be the same, with a retractor muscle, particularly well developed branchial lobes, a spherical larval trunk 0.6–0.8mm long with 2–6 pairs of lateral ampullae and a large oozooid and blastozooid. However, all the zooids initially assigned to this species (Monniot & Monniot, 1987, fig. 20 B, C) may not be conspecific and 2 species could possibly be involved — the second lacking a retractor muscle, but having instead an oesophageal annulus The species resembles *D. listerianum* in the dark spot associated with the neural ganglion, and in the position of the retractor muscle. However, *D. listerianum* has 2 male follicles rather than the undivided testis of the present species. *Lissoclinum roseum* also resembles the present species (see *L. roseum* Remarks)

Diplosoma redika Monniot, 1994 appears to be an aspicular species of *Lissoclinum* — the larva having oozooid and blastozooids toward the posterior end of the trunk.

Diplosoma versicolor Monniot, 1994 from New Caledonia forms colonies with mauve and brown-purple pigments marbled with pale yellow. Lobes overgrow the surface to form complex 3-dimensional shapes with vast common cloacal spaces, the zooids crossing them in connectives between surface and central test. The cloacal apertures are few but large. The zooids have black squamous ectodermal cells, and a dark pigment spot near the dorsal ganglion. Zooids are of moderate size, with longitudinal pharyngeal and parietal muscles, a retractor muscle from the posterior end of the thorax, and the testis is divided into 2. According to Monniot (1994) the species is similar to *D. inflatum* (< *D. translucidum*), but is distinguished by its colour and leaf-like branchial lobes. *D. translucidum* is further distinguished by its tough test, and flat colonies. *D. ferrugeum* lacks the globular colonies of the present species and has conspicuous morulae bodies in the test. The presence of transverse muscles in the parietal thoracic wall of *D. versicolor* (Monniot, 1994) is apparent only, resulting from misinterpretation of artefacts of preservation.

Diplosoma ferrugeum sp. nov.
(Figs 2D, 151, 178H; Pl. 21A)

Leptoclinum macdonaldi: Van Name, 1918: 159.
Not *Diplosoma macdonaldi* Herdman, 1886: 315. Gottschaldt, 1898: 83 (<*D. listerianum*).

TYPE LOCALITY. Queensland (Heron I., rubble fauna, south opposite cay, low tide, coll. P.Kott March 1975, holotype QM G302262; coll. P. Kott March 1993, paratype QM G308027.

FURTHER RECORDS. Western Australia (Montebello Is, WAM 961.93; Houtman's Abrolhos, WAM 200.87). Queensland (Hervey Bay, QM GH1351, GH1357, GH1827, GH1837, GH3834, G9442; Capricorn Gp, QM G9444, GH2262, G301635, G302107, G302134, G302258-9, G302311, G302331, G302503-4, G302509, G302511, G302519, G302556, G302565, G302568, G302952, G302981; Swain Reefs, QM G308379, G308404; Abbot Point, GH5356; Townsville, QM GH3911; Lizard I., QM GH321, G302215, G308351). Lord Howe I. AMPI 280 299, QM GH4379, G302295). Philippines (Van Name, 1918)

COLONY. Colonies form a thin, almost slimy sheet, over the substrate. In life they generally are some shade of brown, tan, or orange with cream or grey streaks or marble pattern in the surface and some clear patches where the orange-buff or yellow test over the zooids can be seen through the surface. Some black pigment is mixed with cream blood cells and orange pigment in the test around the zooids and in the surface. Black squamous epithelum surounds the zooids — most conspicuous over the abdomen and in the anterior part of the thoraces. In preservative the test becomes more translucent owing to the loss of some of the brown pigment from the surface. However, the cream or grey streaks are seen to be caused by opaque white morulae that form clouds in the surface (and especially in the test over the common cloacal cavities) and also are crowded in the test connectives that enclose the zooids and connect the surface to the basal test. These morulae, together with the cream or yellow blood and test cells and irregular brown to black pigment cells, obscure the zooids. The morulae, which appear not to be calcareous (not dissolving in acid), are up to 0.01mm in diameter. They are not spicules with radial rays, but each consists of a more or less spherical oval or egg-shaped mass of small spheres.

Usually, zooids are embedded in the terminal branches of test connectives between the thin surface and basal layers of test. A strand of test from the basal layer subdivides and each subdivision contains one, or 2 or 3 abdomina clumped together, while all the thoraces are separate, surrounded by the thoracic component of a very extensive three-dimensional cloacal cavity which is interrupted only by the test strands enclosing the zooids. In one colony (WAM 961.93) zooids are embedded ventrally in the thicker columns of test (rather than in branching strands) and from the surface the branchial apertures outline the more or less circular to oval translucent brownish areas, which are surrounded by the cream coloured test over the common cloacal canals.

ZOOIDS. Zooids are relatively large, but delicate, held firmly in the test and are impossible to remove. They are about 1.6mm long, even with the abdomen bent up at the side of the posterior end of the thorax. The rim of each branchial aperture is divided into 6 large lobes either deep, or wide and shallow (depending on the state of contraction of the branchial siphon). Each branchial lobe has a sharp, darkly pigmented point protruding from the centre. A small, dark spot is between adjacent lobes. The atrial aperture is very wide exposing the branchial sac to the cloacal cavity and a small black dot is in the mid-dorsal line near the upper rim of the atrial aperture (just beneath the dorsal tubercle). Stigmata are long and narrow, 12–14 have been counted in the anterior row, and they can reduce to 10 in the posterior row. They are lined with delicate, flat, epithelium. A retractor of variable length projects from the posterior end of the thorax. The gut loop is horizontal, bent up against the right side of the thorax. The abdominal wall over the gut and around the anterior prebranchial part of the thorax is brown in preservative owing to the dark squamous epithelium of the body wall. Some dark pigment lines the branchial lobes and the rim of the atrial aperture (which usually is drawn back to a line along each side of the endostyle). In preservative this dark pigment may largely be lost. However, the black dots between and in the points of the branchial lobes, in the mid-dorsal line of the upper rim of the atrial aperture and in the tentacular ring persist in preservative, although often they are faded.

Gonads are beneath the gut loop. The testis consists of 2 follicles with the straight vas deferens curving around between them on their outer surface. The ovum is anterior to the testis. Following fertilisation, the embryo is incubated in the abdomen of the parent zooid. As the embryos develop the zooids appear to regress, and a portion of the gut loop is all that remains, isolated with the embryo in a stalked marsupium that projects up into the cloacal cavity. This is developed from the test connective that once

enclosed the whole zooid. It appears to lose its connection with the surface test and remains connected only to the basal test.

Embryos are present in specimens from Heron I. in March (QM G302262, G302981), August (QM GH2262), October (QM G302952), and November (QM G302331); Abbot Point in March (QM GH5356); and Lizard I. in June (QM G302215). Larvae are large and spherical, the trunk about 1mm in diameter. The tail is wound halfway around it. The 3 antero-median adhesive organs have 4 ectodermal ampullae on each side,

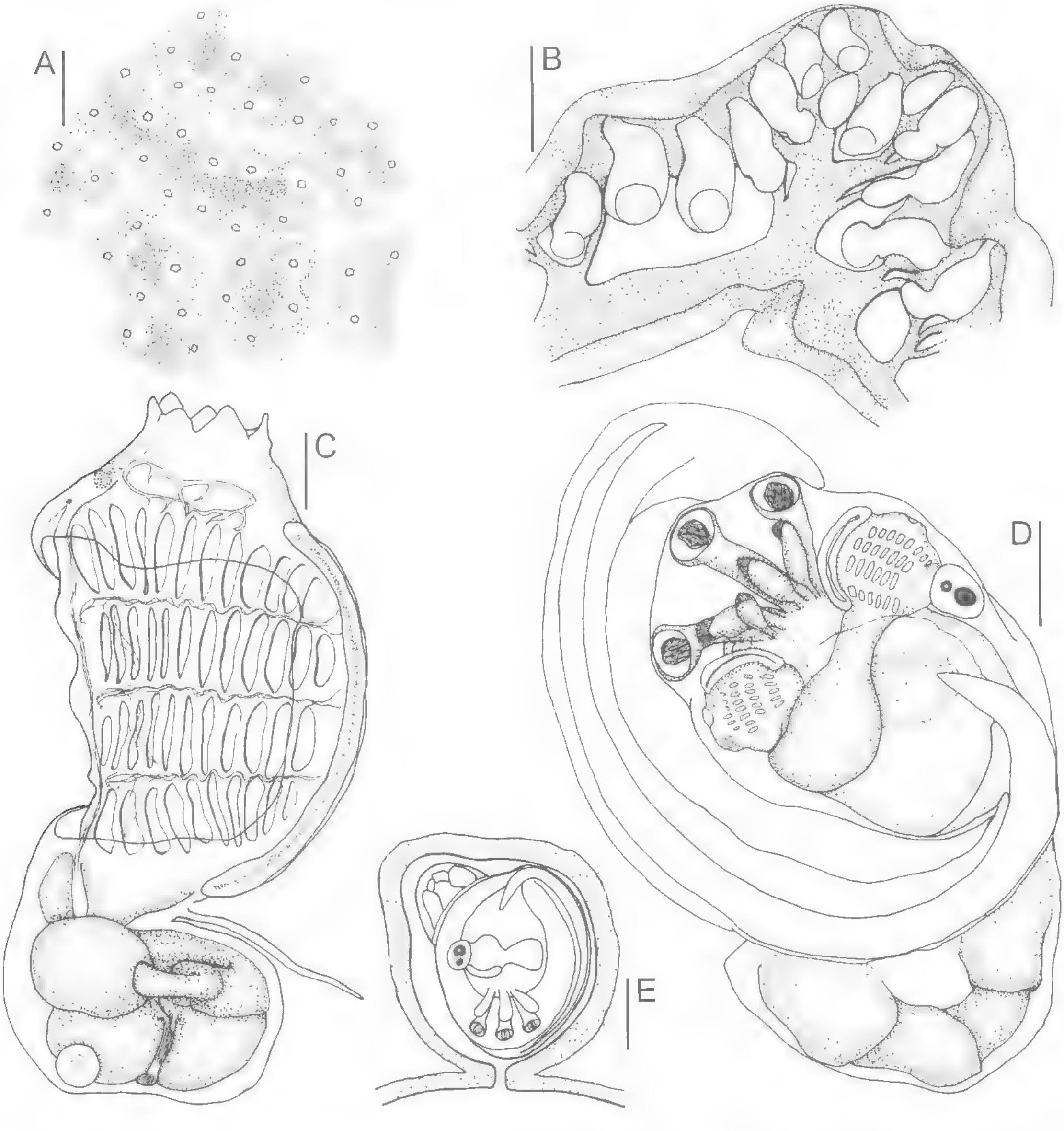


FIG. 151. *Diplosoma ferrugeum* sp. nov. (A, WAM 961.93; B, QM GH4379; C, QM G302311; D,E, QM G302215) – A, surface of colony; B, semidiagrammatic vertical section through colony showing position of zooids and common cloacal cavity; C, zooid; D, larva, in brood pouch with remnants of zooid (gut loop) attached; E, larva in brood pouch, with vestige of parental zooid attached, in stalked marsupium projecting up into the cloacal cavity from the basal test (QM G302215). Scales: A, 1.0mm; B, 2.0mm; C,D, 0.2mm; E, 0.4mm.

and at the anterior end of the trunk, an oozooid and 2 or 3 blastozooids, thoracic buds on the left, abdominal ones on the right. Posteriorly the larval haemocoel is in 2 distinct compartments, one associated with the oozooid, and the other with the blastozooid. The structure of the larva is difficult to determine, being obscured by the test cells and morulae in the larval test.

REMARKS. In preservative this species resembles *D. listerianum*, having the same branched test strands crossing the vast cloacal cavity and dark squamous epithelium with light coloured nuclei in the abdominal and thoracic body wall. However, the present species has yellowish cream refracting bodies in the test which are opaque morulae, obscure the zooids and in life form a cream to grey marble pattern with the tan-brown-black pigment in the surface test. These bodies do not appear to be organic, being present on SEM stubs prepared by incineration of strips of test. Further, *D. listerianum* has smaller zooids (the branchial sac has fewer stigmata), and larvae have a smaller trunk (0.4 –0.6mm long: Rowe, 1966) and fewer ampullae. *D. macdonaldi*: Gottschaldt, 1898 appears (from Gottschaldt, 1898, pl.36 fig.5) to be a specimen of *D. listerianum*, the zooids being clearly seen in a transparent colony, rather than a cloudy one as in the present species. *Leptoclinum macdonaldi*: Van Name, 1918 has, like the present species, 12–14 stigmata per row (more than most other species in this genus) and apparently is conspecific.

D. ata and *D. translucidum* also have almost spherical larvae with oozooid and blastozooid at the anterior end of the trunk. The former species has an undivided testis, but the latter has 2 testis follicles like the present one and *D. listerianum*. However, *D. translucidum* has a tough and fibrous test unlike the delicate test of *D. ferrugeum*, and it lacks the characteristic morulae and the black spot in the neural ganglion.

Monniot (1994) found a black spot in the vicinity of the neural ganglion of *D. ata* and *D. versicolor* that is reminiscent of the dark spot in the median dorsal part of the rim of the atrial aperture of the present species. In *Diplosoma versicolor*, the branchial lobes, zooids with dark dorsal pigment spot near the neural ganglion, 2 testis follicles, and the size of the larval trunk are similar to the present species. *D. versicolor*, has globular colonies rather than thin films and lacks the morulae that are so conspicuous in the present species.

Preserved specimens of *D. ferrugeum* look like *Lissoclinum roseum*, with similar large cloacal spaces crossed by branching strands of test in which zooids are embedded. However, in addition to the generic characters, *L. roseum* lacks the morulae of *D. ferrugeum* and its embryos are brooded in a pouch constricted off from the abdomen (rather than projecting into the common cloacal cavity from the basal test).

Diplosoma listerianum (Milne Edwards, 1841)
(Fig. 152; Pl. 21B,C)

Polyclinum sp. Lister, 1834: 382.
Leptoclinum listerianum Milne Edwards, 1841: 295. Alder & Hancock, 1912: 48.
Diplosoma listerianum: Michaelsen, 1919: 41 (var. *gelatinosum*). Hartmeyer, 1924: 172. Thompson, 1934: 17. Berrill, 1950: 125. Kott, 1952: 80; 1981: 190; 1998: 84. Millar, 1952: 51; 1955: 190; 1962: 170. Carlisle, 1953: 61. Rowe, 1966: 458. Monniot, C. & Monniot, F., 1997: 1629.
Pseudodidemnum listerianum: Della Valle, 1877: 47.
Diplosoma listeri Lahille, 1890: 104.
Didemnum gelatinosum Milne Edwards, 1841: 295.
Diplosoma gelatinosum: Lahille, 1890: 104. Pizon, 1905: 1. Harant & Vernières, 1933: 73. Pérès, 1949: 40.
Leptoclinum gelatinosum: Alder & Hancock, 1912: 48.
Leptoclinum punctatum Forbes, 1848: 48. Alder & Hancock, 1912: 48.
Diplosoma punctatum-listeri: Lahille, 1890: 110.
Diplosoma rayneri Macdonald, 1859: 373. Kott, 1962: 305.
Pseudodidemnum crystallinum Giard, 1872: 656.
Diplosoma crystallinum Drasche, 1884: 40.
Astellium spongiforme Giard, 1872: 657.
Diplosoma spongiforme: Lahille, 1890: 104.
Diplosoma carnosum Drasche, 1884: 39.
Diplosoma chamaelean Drasche, 1884: 40.
Pseudodidemnum zosterarium Jourdain, 1885: 1513.
Diplosoma macdonaldi Herdman, 1886: 315. Gottschaldt, 1898: 657. Van Name, 1902: 368; 1921: 335; 1924: 26; 1930: 440; 1945: 109. Brewin, 1946: 100; 1950a: 345; 1951: 104; 1952: 188; 1958: 439; 1960: 119.
Leptoclinum macdonaldi: Hartmeyer, 1909: 1454. Van Name, 1921: 335; 1924: 26. Grave, 1927: 218; 1928: 274. Berrill, 1932: 77.
Not *Leptoclinum macdonaldi*: Van Name, 1918: 159 (<*D. ferrugeum*).
Diplosoma mitsukurii Oka, 1892: 265; 1927: 500. Nishikawa & Tokioka, 1976: 386. Tokioka & Nishikawa, 1975: 326.
Leptoclinum mitsukurii: Tokioka, 1953: 201; 1954: 249; 1967: 100; 1962: 7.
Diplosoma lacteum Van Name, 1902: 369.
Leptoclinum lacteum: Hartmeyer, 1909: 1455.
Diplosoma atropunctatum Van Name, 1902: 370.
Leptoclinum atropunctatum: Hartmeyer, 1909: 1455.
Diplosoma pizoni Ritter & Forsyth, 1917: 474. Van Name, 1945: 110.
Leptoclinum okai Tokioka, 1949a: 5.
Leptoclinum macrolobium Tokioka, 1949b: 44.

NEW RECORDS. Western Australia (Enderby I., WAM 959.88; Albany, QM GH5466). South Australia (St Vincent Gulf, QM GH1306; York Peninsula, QM GH2400, GH2408, G302880). Victoria (Bass Strait, QM G11855); New South Wales (Port Kembla, QM GH2005-6; Shell Harbour, QM G304569). Queensland

(Tallebudgera, QM GH5190, G301678; Moreton Bay, QM G302716, G302719, G308350; Heron I., QM G302313, G308149, G308314; Townsville, QM GH2097, GH4658, G301634; Lizard I. QM G308356).

PREVIOUSLY RECORDED. North Sea, Irish Sea, English Channel (Lister, 1834; Milne Edwards, 1841; Forbes, 1848; Giard, 1872; Alder & Hancock, 1912; Michaelsen, 1919; Hartmeyer, 1924; Thompson, 1934; Berrill, 1950; Carlisle, 1953; Millar, 1952). Mediterranean Sea (Giard, 1872; Della Valle, 1877; Lahille, 1890; Harant & Vernieres, 1933). Adriatic Sea (Drasche, 1883-4). Atlantic Ocean (Brazil – Herdman, 1886; Bermuda – Van Name, 1902; Caribbean – Van Name, 1921, 1930, 1945; Grave, 1927-8; Berrill, 1932; West Africa – Michaelsen, 1919; Pérès, 1949). South Africa (Millar, 1955, 1962; Michaelsen, 1915). Indian Ocean (Monniot, C. & Monniot, F., 1997). California (Ritter & Forsyth, 1917). Japan (Oka, 1892, 1927; Tokioka, 1949a,b, 1953; Nishikawa & Tokioka, 1976; Tokioka & Nishikawa, 1975). Indonesia (Gottschaldt, 1898). Fiji (Kott, 1981). New Zealand (Brewin, 1946, 1950a, 1951, 1952, 1958, 1960). Western Australia (Cockburn Sound – Kott, 1962). Victoria (Western Port – Kott, 1966). New South Wales (Port Jackson – Macdonald, 1859).

D. listerianum is truly cosmopolitan, recorded from tropical to temperate waters of the Pacific, Atlantic and Indian Oceans and the Mediterranean and North Seas.

COLONY. Colonies are soft, thin, translucent sheets to more complex lobed masses that cover extensive areas of hard and soft substrates including weed (*Zostera* blades and *Halimeda*). Often they grow over living, moving organisms, attached to the hard shells of molluscs and the exoskeletons of crustaceans. These sessile colonies are thus endowed with the advantages of movement. Specimens from Moreton Bay (QM G308350, G302719) were found respectively on the limbs of a spider crab (*Hyastenus diacanthus*) and almost completely covering a small crab — on its back, rostrum and the backs of the legs, being absent only from the terminal joints of the legs and the eyes and eye-stalks. Brown-black-green to white zooids are visible through the grey, translucent to transparent test. The dark colour results from the black squamous epithelium often on the abdomen and sometimes also on the thoraces, especially anteriorly. Zooids appear as white dots when the epithelium is not black. One colony (QM G302880), although soft and mutilated in preservative, appears from its photograph to be more robust in life and has elevated cones and ridges on the surface with common cloacal apertures terminal or evenly spaced along the tops of the ridges. This colony is a reddish rusty colour in preservative, although usually specimens are grey in preservative. Between the thin layer of surface and basal test

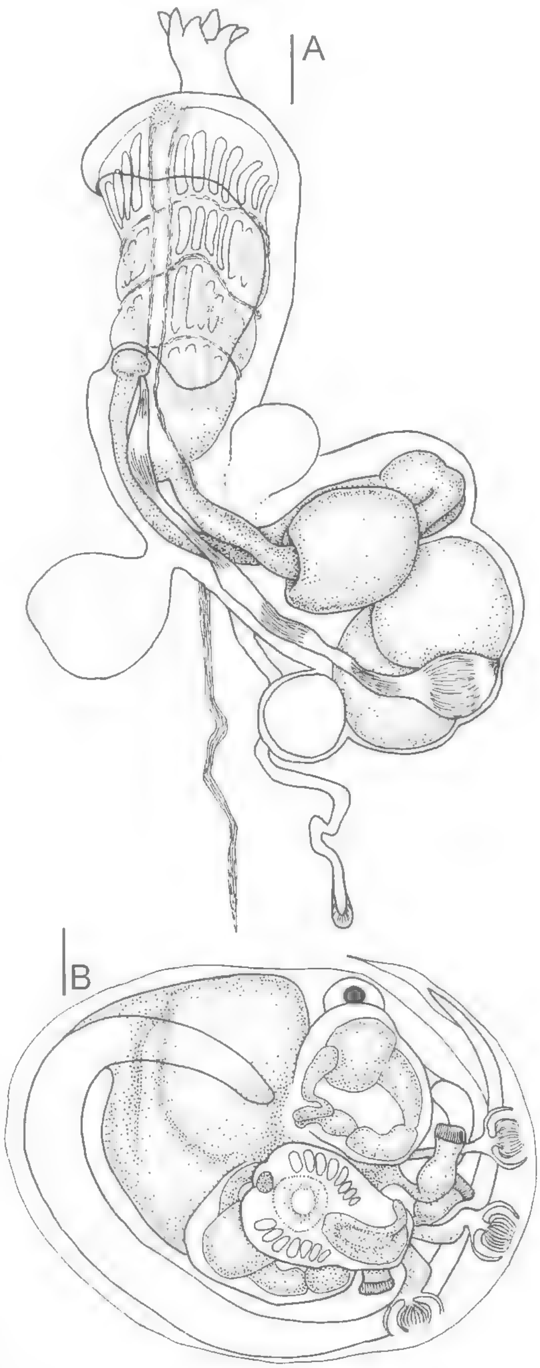


FIG. 152. *Diplosoma listerianum* (QM G301678) – A, zooid from dorsal surface showing oseophageal buds and proximal part of vas deferens expanded to serve as a seminal vesicle; B, larva showing cerebral vesicle, blastozooids and terminal columnar epithelum on tips of club-shaped ectodermal ampullae. Scales: 0.1mm.

the extensive common cloacal cavity is crossed by thin test connectives in which the zooids are contained. Occasionally a test connective may branch at its base, each branch supporting a zooid at the surface. Each zooid is entirely isolated in a single branch or strip of test and abdomina are never clumped together in the basal connective. White granular bodies to about 0.02mm diameter embedded in the test, especially around the zooids give it a cloudy appearance, but there is no pigment except the black squamous epithelium often present on the zooids. Living colonies have a more robust appearance than preserved ones owing to the water pressure in the cloacal cavity.

ZOOIDS. Zooids are about 1mm long. A small, intense, dark median spot is in the dorsal mid-line just anterior to the atrial aperture, although this may fade in preservative. A short retractor muscle projects from the posterior end of the thorax. The branchial siphon is conspicuous with 6 deeply divided, pointed lobes around the rim of the opening. The atrial opening is a large, sessile opening exposing most of the branchial sac directly to the cloacal cavity. Ten stigmata are in anterior row, reducing to 8 in the posterior row. Conspicuous stolonic vessels with terminal ampullae project from the ventral side of the abdomen where the post-pyloric part of the gut loop is bent ventrally at right angles to the vertical axis of the zooids. These stolonic vessels extend through the test toward the base of the colony. A tapering retractor muscle projects from about halfway down the oesophageal neck. Two oval testis follicles are against the dorsal (or posterior side) of the flexed part of the gut loop. The vas deferens is hooked around between them, extending anteriorly along the vertical part of the ascending limb of the gut loop. The proximal part of the vas deferens where it hooks around the outside of the 2 testis follicles is expanded into a club-shaped seminal vesicle.

Embryos are present in newly recorded specimens in October (QM GH5190, G301678), November (QM G308350) and April (QM G302719) in SE Queensland; June (QM G308356) at Lizard I. and August (QM GH2408) in St Vincent Gulf. They often are crowded, in the basal test but occasionally (QM G302719) also are in the strands of test behind the zooids. The larval trunk is almost spherical, and about 0.7mm long with the tail wound three quarters of the way around it. A complete blastozooid, with the oozooid, 2 pairs of urn-shaped ectodermal ampullae and 3 median adhesive organs are in the anterior half of the trunk. Large bladder cells are in the larval test, and the granular white bodies that make the adult test cloudy and translucent also are in the larval test. In living specimens a band of white material is deposited around the posterior end of the trunk and in the test vane around the tail epidermis.

In one living specimen (QM G302719), larvae were observed being released from the basal test into the common cloacal cavity and out through the common cloacal apertures. They swim very rapidly, the tail moving in a sculling motion. A video estimate of the frequency of its more or less circular beat was in excess of 25 times a second.

REMARKS. *D. macdonaldi* Herdman, 1886 is from Brazil in shallow waters. It is described as a thin soft and flexible colony loosely attached to the branches of a hydroid with brownish patches in an otherwise colourless test, and opaque grey zooids. The black/brown pigment that Rowe (1966) referred to as forming a pattern around the abdominal region, is in fact the squamous epithelium with pale nuclei.

Although Rowe (1966) discounted the form of the colony as a distinction between species there do appear to be significant differences between the present species and species with firmer colonies and more restricted cloacal systems such as *D. modestum* (Michaelsen, 1920) from the Seychelles and Zanzibar, which has firm test like *D. simile* from which it is distinguished by the lack of *Prochloron*. It does not appear to be a synonym of the present species, although Michaelsen thought it was conspecific with *D. spongiforme* (Giard, 1872).

The absence of black squamous epithelium and the black pigment spot from long-preserved specimens may result in confusion with *D. translucidum*. However, *D. translucidum* has larger larvae with 3 pairs of ectodermal ampullae, firmer colonies, shallower common cloacal cavities and shorter terminal branches of test connectives so that zooids are clumped together at the surface.

Diplosoma simile (Sluiter, 1909)
(Fig. 153; Pl. 21D)

Leptoclinum simile Sluiter, 1909: 77.
Diplosoma similis: Kott, 1980: 26; 1981: 191; 1982a: 117. Monniot & Monniot, 1987: 62. Monniot, 1994: 9.
Diplosoma simile: Kott, 1998: 85.
Diplosoma virens: Eldredge, 1967: 228. Millar, 1975: 241. Kott, 1977: 620 (part). Thorne, Newcomb & Osmond, 1977: 575.
Leptoclinum midori Tokioka, 1954: 11.
Diplosoma midori: Kott, 1980: 29.

NEW RECORDS. Western Australia (Rowley Shoals, WAM 1055-83; Kendrew I., WAM 1056.83). NSW (Hastings Point, QM GH939). Queensland (Capricorn Group, QM GH2258, G302517; Orpheus I., QM G302322; Hardy Reef, QM GH2071; Lizard I., QM G308355). Western Pacific (Truk Lagoon, QM GH813). Papua New Guinea (Madang, WAM 399.92). Timor Sea (Ashmore Reef, WAM 519.92).

PREVIOUSLY RECORDED. Queensland (Heron I.–QM G9883 Kott, 1980; Magnetic I., Green I., Lizard I., Carter Reef, Sue I. – Kott, 1977, 1980, 1982a). Western Pacific (Caroline Is, Palau Is, Guam – Kott, 1982a; Philippines – Millar, 1975, Kott, 1982a; New Caledonia – Monniot, 1994). Central Pacific (Hawaii, Eniwetok, Marshall Is, Palmyra – Eldredge, 1967; Line Is – Eldredge, 1967, Kott, 1980; Christmas I. – Kott, 1980; Fiji – Kott, 1980, 1981; Tonga – Kott, 1980). Indonesia (lectotype ZMA TU591.1 Sluiter, 1909). Singapore (Kott, 1982a). Japan (Tokhara Is – Tokioka, 1954).

The species is common near the reef edge (in the surf zone) where it encrusts under-surfaces of the reef canopy and can be seen encroaching through gaps onto the upper surface of the reef. It also grows amongst deep accumulations of rubble, binding it together. At low latitudes it sometimes is found exposed directly to the light.

COLONY. Colonies form robust encrusting sheets (about 2mm thick) that often are very extensive. They adhere closely to, and the basal test thickens to fill irregularities in, the substrate. The thickness of the colony is therefore irregular, although the surface is smooth, almost slippery, and even. The consistency of the test is gelatinous but firm and the colony often continues its growth in one plane beyond the margin of the substrate to span gaps between adjacent surfaces. Consequently this species has the capacity to bind coralline, and other rubble together. In life the colony is translucent and almost any shade of green to dark blackish-blue, or green with blue iridescence on the surface. The colour often varies according to the angle of the light falling on it and also maybe affected by the colour of the *Prochloron* (in the common cloacal cavity) and/or some structural property of the surface. Sometimes white or pinkish white deposits (calcareous?) are in the test.

The surface layer of test (including a superficial layer of bladder cells), the common cloacal cavity around the thoraces (which cross it independent of one another), and the thick basal test (in which abdomina are embedded), each occupy one-third of the thickness of the colony, although the basal test is sometimes thicker. In the centre of some of the larger colonies the common cloacal cavity is deeper and the whole zooid (rather than just the thorax) is suspended in a test strand connecting the surface with the basal test. Zooids are evenly spaced. *Prochloron* line the cloacal cavity. They can be removed only by strong pressure, but this

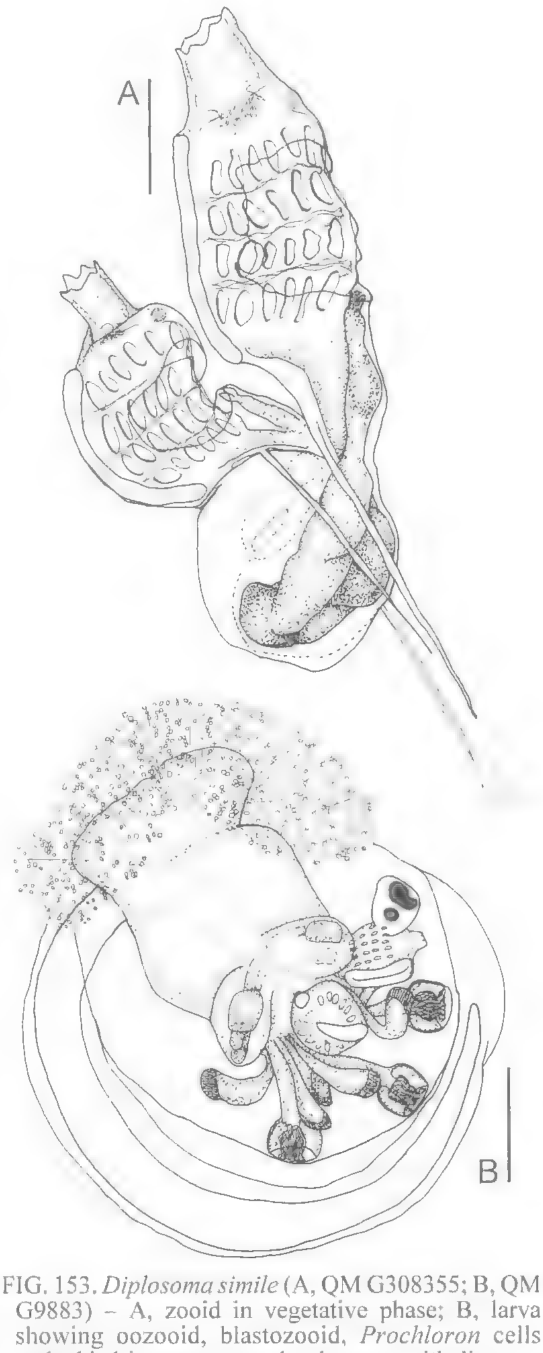


FIG. 153. *Diplosoma simile* (A, QM G308355; B, QM G9883) – A, zooid in vegetative phase; B, larva showing oozooid, blastozooid, *Prochloron* cells embedded in rastrum, and columnar epithelium on tips of club-shaped ectodermal ampullae. Scales: 0.2mm.

causes lysis of test cells and generation of acid which causes their death (Parry, 1984b).

ZOOIDS. Zooids are about 1mm long. The branchial siphon is well-developed with a conspicuous sphincter muscle and 6 triangular lobes around the rim of the aperture. The atrial aperture is large exposing most of the brancial sac directly to the cloacal cavity. A retractor muscle projects into the test from the posterior end of the thorax. Four rows of 6 stigmata are in the branchial sac . The abdomen bends at right angles to the longitudinal axis of the thorax at the base of the moderately long oesophageal neck. Black squamous epithelium is on the abdominal body wall although it often fades in preservative. The stomach is long, oval and occupies most of the proximal limb of the gut loop. A long duodenum and a short posterior stomach are in the pole of the gut loop. The vas deferens is straight except at its proximal end where it curves around between the 2 lobes of the testis.

The species is prolific, larvae being in the basal test of colonies collected in July, February, December and March at Heron I., August at Green I. (Kott, 1980), July and August in Fiji (Kott, 1980), October and November in the Truk Lagoon (Kott, 1980, 1982a), January at Guam (Kott, 1982a) and February at Christmas I. (Kott, 1982a). They are large, the trunk 0.8mm long, excluding the posteriorly projecting rastrum. The thorax of the oozooid projects up into the larval test with the large cerebral ganglion protruding from its upper surface. The thorax of the blastozooid, and the ectodermal ampullae and adhesive organs project from the left side of the anterior margin of the trunk and are separated from the oozooid by a deep cleft in its anterior margin. Three or 4 pairs of long slender flexible ectodermal ampullae with round tips on which columnar ectodermal cells form a cap, project from each side of the 3 median adhesive organs. The T-shaped rastrum, with its overlying test modified into a brush of long hairs (Kott, 1980, 1982b) projects from the middle of the postero-dorsal end of the trunk, just above the insertion of the tail. The tail winds about two-thirds to almost the whole way around the trunk.

REMARKS. This species is one of the most common of the didemnid-*Prochloron* obligate symbioses in the tropical Pacific. It has not yet been recorded from west of Singapore, nor from Western Australia.

Some of its smaller colonies could be mistaken for *D. virens*, although they are readily distinguished by the more extensive thoracic common cloacal cavities in the present species and the origin of the retractor muscle from the posterior end of the thorax (rather than halfway down the oesophageal neck). The larval trunk of the present species (to 0.8mm long), is shorter than that of *D. virens*, and the tail is longer. There is no significant difference between the present species and *D. midori* Tokioka, 1954.

Diplosoma translucidum (Hartmeyer, 1909)
(Fig. 154; Pl. 21E)

Leptoclinum perspicuum Sluiter, 1909: 79.
Leptoclinum translucidum Hartmeyer, 1909: 1490 (nom. nov. for *L. perspicuum*).
Not *Leptoclinum translucidum*: Kott, 1962: 306 (=*D. velatum*).
Diplosoma translucidum: Hartmeyer, 1919: 125. Kott, 1998: 85 (part, not specimens from Bass Strait or SW coast).
Not *Diplosoma translucidum*: Kott, 1975: 10; 1976: 72 (=*D. velatum*).
Diplosoma inflatum Monniot, 1994: 5.

NEW RECORDS. Western Australia (Cape Rutheres, QM G302946; NNE Dampier Archipelago, WAM 5.93) Queensland (Hervey Bay, QM G9440, G9443, GH2260, Capricorn Group, QM GH759, GH2259, G301691, G308349; Lizard I.,QM G301542, G302027, G302030-1; 17°03'S 146°07.8'E, QM GH2345)

PREVIOUSLY RECORDED. Western Australia (Cape Jaubert – Hartmeyer, 1919). Indonesia (Sluiter, 1909). New Caledonia (Monniot, 1994).

Recorded colonies are from low tide to 160m (Hartmeyer, 1919).

COLONY. Colonies are fleshy and firm sheets, and the test is tough, fibrous and does not tear readily. In life the test is clear to translucent and rufus[R] with flesh[R] to orange or red-brown zooids showing through. In preservative, at first the test is cloudy and the zooids pink-beige to pinkish-brown with a brown gut loop and embryos. After long-term preservation the colonies are light grey, with white zoods showing through the translucent test. A yellowish-white ring of granules surrounds each of the relatively numerous large sessile common cloacal apertures was observed in one colony (WAM 5.93). Both surface and basal layers of test are thin. Zooids are held at the surface by their separate branchial siphons. The whole zooid sometimes is separated from others but the terminal branches of test connectives are short, keeping zooids together and often the abdomina are not separated from one another, the abdomina of each group of 2-6 zooids usually being clumped together in common test and attached to the basal test by a single connecting strand. The primary cloacal cavities extend around and posterior to each

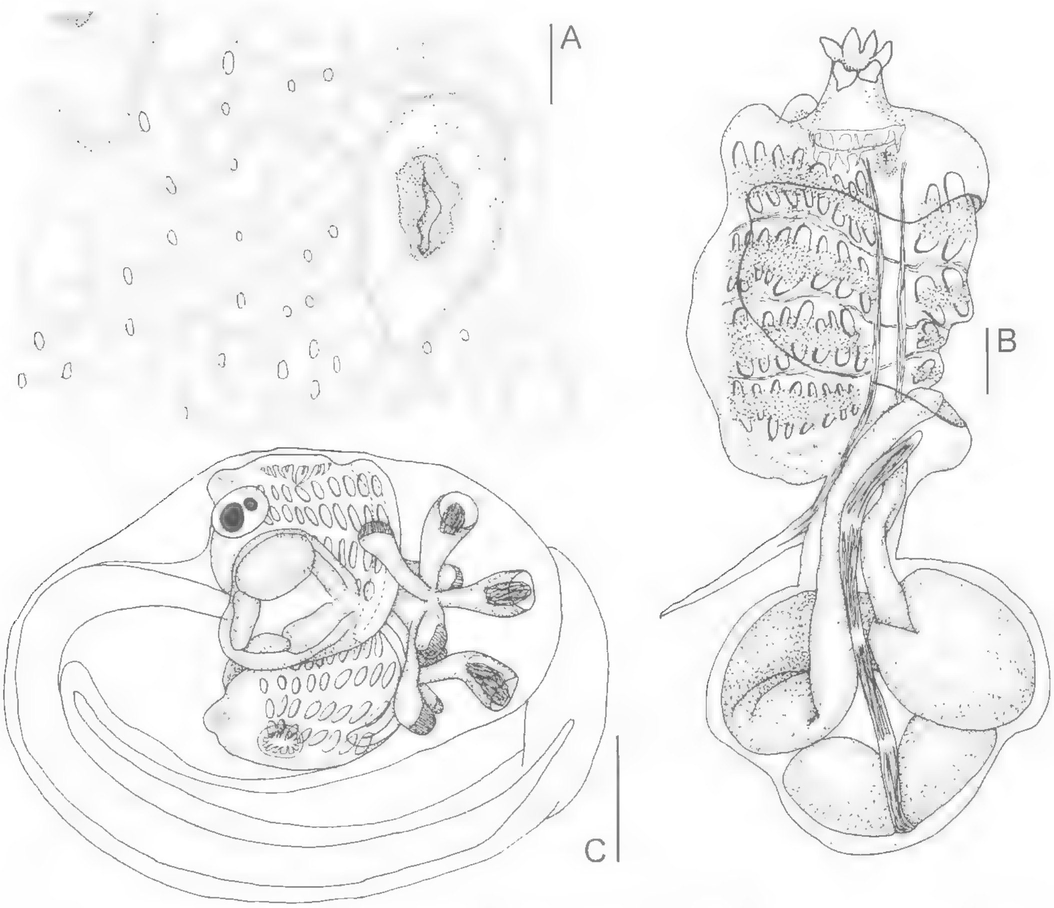


FIG. 154. *Diplosoma translucidum* (A, WAM 5.93; B, QM G308349; C, QM G301542) – A, surface of colony; B, zooid; C, larva showing oozooid, blastozooid and columnar epithelium on tips of club-shaped ectodermal ampullae. Scales: A, 1.0mm; B,C, 0.1mm.

clump of zooids, interrupted only by the vertical connective between each zooid clump and the basal test. Secondary cloacal canals penetrate each clump of zooids at thoracic level. Colonies are thicker in life than in preservative owing to the inflated common cloacal cavity. Embryos are in the basal test. The large common cloacal apertures are randomly placed over junctions of deep primary canals that separate each clump of zooids. Zooids are difficult to remove from the tough fibrous test of the preserved colonies.

ZOOIDS. Zooids are relatively small, the thorax being only about 0.5mm long. The oesophageal neck is relatively long and the distal half of the abdomen, from the level of the stomach, bends at right angles to the longitudinal axis of the zooids to lie horizontally. Dark squamous epithelium is on the abdomen but is not always evident. The branchial siphon is cylindrical, and the aperture is fringed with 6 long finger-like lobes. When contracted the rim of the aperture between these lobes projects out like an accessory lobe. A moderately long, narrow retractor muscle projects from the posterior end of the thorax. The atrial aperture is wide, exposing most of the branchial sac directly to the cloacal cavity. Ten stigmata are in the anterior row in the branchial sac, reducing to 8 in the posterior row. The stomach lies more or less obliquely where the abdomen bends horizontally, and the duodenum, large posterior stomach and the proximal part of the rectum form the horizontal part of the gut loop. A constriction halfway up the rectum was not observed, nor were gastric vesicles seen around the gut. The testis, underneath the horizontal part of the gut loop, consists of 2 follicles side by side. Their short vasa efferentia, one from the inner margin of each follicle, near its

postero-ventral border, join to form the vas deferens which curves around between the follicles, extends straight anteriorly between oesophagus and rectum, and opens near the anus. The ovum is dorsal to the testis, but moves down the test connective into the basal test at an early stage, presumably following fertilisation. The proximal end of the vas deferens sometimes is swollen into a large seminal vesicle.

Embryos are in the basal test of colonies taken off Cairns (QM GH2345) in January, Lizard I. (QM G301542, G302027, G302030-1) in June, off the northern tip of Western Australia (QM G302946) in August, the Capricorn Group (QM G308349, GH759) in November and Hervey Bay (QM G9440) in November. Larvae are large, the trunk 0.8mm long, with a relatively long narrow tail wound three quarters of the way around it. The anterior three quarters of the trunk is occupied by a large oozooid and one or 2 blastozooids of more or less equal size (each with 4 well developed rows of stigmata), 3 median adhesive organs (with long narrow flexible stalks and deep tulip-shaped terminal cups and axillary cones), and 2 or 3 ectodermal ampullae per side (each with columnar ectoderm on the expanded, almost globular tip). The cerebral vesicle (with ocellus and otolith) protrudes dorsally from the oozooid. Well advanced larvae prior to liberation are found in pouches projecting up into the common cloacal cavity from the basal test (QM G302946). Presumably they are liberated into the cloacal cavity by rupture of these pouches.

REMARKS. The species is characterised by its tough test, relatively small zooids, abdomen posterior to the thorax (not folded up against it), tightly clumped zooids — each clump with a single, unbranched test connective crossing the cloacal cavity to the basal test, narrow pointed branchial lobes, and large larvae with well advanced oozooid and blastozooids. The latter resemble *D. ata* Monniot & Monniot, 1987, which has a retractor muscle but only one testis follicle.

The New Caledonian specimens (as *D. inflatum*) of the present species differ from the newly recorded ones in having 12 (rather than 10) stigmata in the anterior row — although there is some inconsistency in the numbers shown (Monniot, 1994, fig. 2A,C), and a shorter larval tail. These differences probably are not of sufficient significance to indicate a separate species, especially in view of compelling similarities such as the general form of larvae, zooids, colony organisation, and fibrous test.

The present species lacks the black pigment spot near the dorsal tubercle found in *D. versicolor* Monniot, 1994. It is distinguished from *D. listerianum* and *D. ferrugeum* (which have similar larvae) by its more restricted cloacal cavity, unbranched connectives between the large clumps of zooids and basal test and its tough fibrous test. Embryos of the present species (like those of *D. listerianum*), develop in the basal test rather than in the test connective attached to the floor of the cloacal cavity as in *D. ferrugeum*.

Colonies of the temperate species, *D. velatum* (>*D. translucidum*: Kott, 1962, 1975, 1976), have the same narrow finger-like branchial lobes, number of stigmata per row, 2 male follicles, retractor muscle originating from the posterior end of the thorax, and they lack a pigment spot associated with the dorsal tubercle. The test of *D. velatum* is much softer than the present species, however, and its test connectives are branched as in *D. listerianum* and *D. ferrugeum*.

The colonies described by Sluiter (1909) and Hartmeyer (1919), with zooids showing as white flecks through tough, light grey/translucent test are not significantly different from the Australian and New Caledonian specimens. Sluiter specifically mentions the 6 lobes of long branchial siphons. Hartmeyer referred to the tough test, and both observed the ectodermal vessels and their terminal ampullae in the basal test.

Rowe (1966) suggested that *Leptoclinum perspicuum* (Giard, 1872) (originally *Astellium*) was not considered congeneric with *L. perspicuum* Sluiter, 1909, and thus Sluiter's name is not a homonym and is still the valid name for the present species. However, Hartmeyer (1909) removed *L. perspicuum* (Giard, 1872) to *Didemnum* after Sluiter (1909) had erected *L. perspicuum* Sluiter, 1909. Hartmeyer (1909) correctly provided a replacement name (*L. translucidum*) for Sluiter's species.

Diplosoma velatum sp. nov.
(Fig. 155; Pl. 21F,G)

Leptoclinum translucidum Kott, 1962: 306.
Diplosoma translucidum: Kott, 1975: 10; 1976: 72; 1998: 85 (part, specimens from Bass Strait and SW Australia).

TYPE LOCALITY. South Australian (York Peninsula, Point Turton jetty piles on *Posidonia* seagrass 3-4m, coll. K.L. Gowlett Holmes, W. Zeidler. 16.3.94, holotype SAM E2612; Edithburgh, sand flat with sea grass, 5m, coll. AIMS Bioactivity Group 9.2.89, paratype QM G302909).

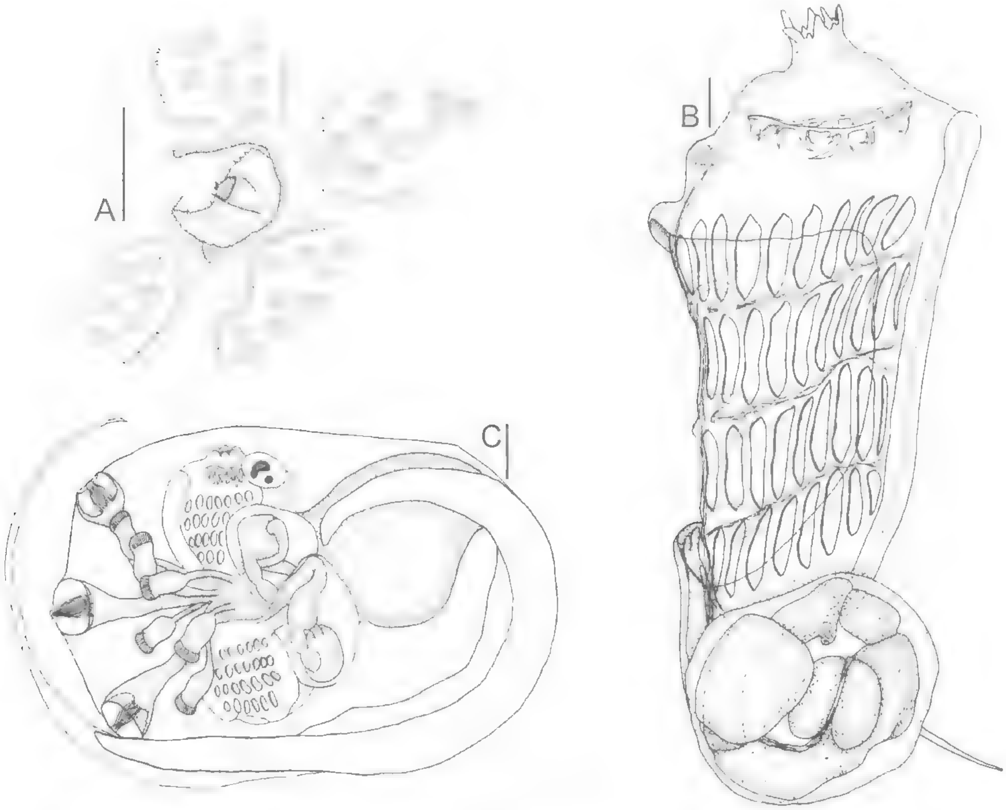


FIG. 155. *Diplosoma velatum* sp. nov. (A, WAM 1155.88; B, SAM E2612; C, SAM E2687) – A, surface of colony; B, zooid; C, larva. Scales: A, 1.0mm; B, C, 0.1mm.

FURTHER RECORDS. Western Australia (Esperance, WAM 1155.88). South Australia (Tipara Reef, QM GH3707, GH3753; Eyre Peninsula, SAM E2687; Cathedral Rock, SAM E2832; Kangaroo I., QM G302911, SAM E2587).

PREVIOUSLY RECORDED. Western Australia (Oyster Harbour – Kott, 1962). South Australia (Investigator Strait – Kott, 1975). Victoria (Western Port – Kott, 1976).

COLONY. Colonies are extensive fleshy sheets or regular, flat to rounded or oval plates or lobes, often found encrusting sea-grass. The test is soft and even slimy, but the colonies are turgid, more or less holding their shape in preservative. In preservative they are up to 5mm thick and may be even thicker in life when the common cloacal cavities are fully inflated. Zooids are in crowded groups or double rows of up to 20 divided into sub-groups of 5–8 zooids. Groups of zooids are visible through the translucent test as patches of white flecks separated from one another by narrow zooid-free strips over the common cloacal canals. Abdomina of zooids in each of the sub-groups are sometimes embedded together in a branch of the single flat test connective that anchors the whole group to the basal or central plate of test, although the thoraces are separate from one another, attached to the surface test by their branchial apertures and sheathed ventrally by separate terminal branches of the test connectives. In other colonies both the abdomina and thoraces are separate, each in a terminal branch of the test connective. The common cloacal cavity is vast, extending the full depth of the zooids around each sub-group, and even more deeply around each major grouping of zooids where the cavity extends behind the zooids to surround the basal common test connectives. Common cloacal apertures are circular when open and fairly regularly spaced about 1cm apart.

The vascular appendages from each zooid extend deep into the test connectives where their elongate terminal ampullae are evident. The test is transparent, almost glassy but slightly pink and cloudy in preservative. There are no spicules. Living colonies are orange.

ZOOIDS. Zooids are of moderate size, to 1.5mm long with a large thorax, long oesophageal neck,

and shorter abdomen. Branchial apertures are small on short siphons with a delicate sphincter muscle and 6 narrow, pointed lobes. When the apertures are contracted the rim of the opening between the narrow lobes is thrown up into a small projection. Ten stigmata are in the anterior row in the branchial sac. The gut loop is horizontal, behind the branchial sac and there are 2 male follicles with a straight vas deferens, its proximal end in the groove between them. A long, narrow retractor muscle projects from the posterior end of the thorax. Zooids are white in preservative and do not have dark squamous epithelium over either thorax or abdomen.

Embryos are present in specimens from Oyster Harbour (Albany) collected in December, Kangaroo I. (QM G302911) in January, the Eyre Peninsula (SAM E2687) in February and Tipara Reef (QM GH3707, GH3753) in May. The larval trunk is large (1.0–1.2mm long) with blastozooids and 3 finger-like ectodermal ampullae each side of the 3 urn-shaped, antero-median adhesive organs (Kott, 1962). The ocellus is in a small papilla-like protrusion from the oozooid about halfway along the dorsum, but the otolith lies beneath it obscured by the small opaque inclusions in the larval test. The tail winds halfway around the trunk.

REMARKS. Kott (1962) assigned specimens of this species (from Albany) to the tropical *D. translucidum*, invoking the large common cloacal cavity as a character of the latter species. Although such a cloacal cavity occurs in *D. listerianum*, *D. ferrugeum* and certain *Lissoclinum* spp., the common cloacal cavity of *D. translucidum* is more restricted and the basal test connectives are unbranched. The test of *D. translucidum* is much tougher, and the colonies have a blue-grey shimmer (Sluiter, 1909; Hartmeyer, 1919) rather than the faint pink colour of the preserved colonies of the present species. Larvae of the present species are larger than those of *D. translucidum* but otherwise are similar. The branchial lobes are narrower and tentacular unlike the broad leaf-like ones of *D. listerianum* and *D. ferrugeum*.

Diplosoma virens (Hartmeyer, 1909)
(Fig. 156; Pl. 21H)

Diplosoma viride Herdman, 1906: 341.
Leptoclinum virens Hartmeyer, 1909: 145-6. Tokioka, 1942: 500; 1967: 68. Kott, 1966: 291.
Diplosoma virens: Hastings, 1931: 102. Newcomb & Pugh, 1975: 533. Thinh & Griffiths, 1977: 673. Thinh, 1978: 617. Kott, 1980: 22, figs 27-30; 1981: 193; 1982a: 114; 1998: 85. Monniot, 1994: 10.
Not *Diplosoma virens*: Eldredge, 1967: 228. Kott, 1977: 620. Thorne, Newcomb & Osmond, 1977: 575 (< *Diplosoma simile*).
Not *Leptoclinum viride* Herdman, 1906: 340 (< *Didemnum viride*).
Leptoclinum simile Sluiter, 1909: 77 (part).
Leptoclinum varium Sluiter, 1909: 80.
Leptoclinum calificiforme Sluiter, 1909: 82. Van Name, 1918: 160.
Diplosoma pavonia Monniot & Monniot, 1987: 60.
?*Diplosoma matie* Monniot & Monniot, 1987: 58.

NEW RECORDS. Western Australia (Shark Bay, WAM 1057.83). Queensland (Capricorn Group, QM G301902, G302448; Swain Reefs, QM G308405, G308416 Magnetic I.; Lizard I., QM G302348). Northern Territory (Cape Don). Western Pacific (West Caroline I., QM GH816).

PREVIOUSLY RECORDED. Queensland (QM G9937 Heron I., QM G12484 Green I., Lizard I., Sue I. – Kott, 1977, 1980 1982a; Low Is – Hastings 1931). Northern Territory (Darwin – Kott, 1980). Western Pacific (Caroline Is, Palau Is, Kiribati, Marshall Is, Philippines – Van Name 1918, Tokioka, 1942 1967, Kott, 1980 1982a; Solomon Is – Monniot, 1994; Fiji – QM G12485 Kott, 1980, 1981; French Polynesia – Monniot & Monniot, 1987). Indonesia (*Leptoclinum varium* ZMA TU597, TU599.6, TU599.8; *L. calificifome* ZMA TU573; *L. simile* ZMA TU591.2 Sluiter, 1909). Indian Ocean (Sri Lanka – Herdman, 1906).

The greatest depth recorded for the species is off Amboina at 40m (Sluiter, 1909: ZMA TU599.6). It is known to occur on the open reef flat on the side of tidal pools in Fiji (Kott, 1981) and along the reef edge and in surge channnels around the base of stands of living coral to 5m.

COLONY. Colonies are small circular to oval cushions from 0.5–2cm long and 2–5mm thick. Smaller colonies are almost spherical but larger ones are almost flat on the upper surface, with a depression in the centre from which the common cloacal aperture protrudes on a conical or cylindrical chimney which often is bent in the direction of the prevailing current. The upper rim of the opening may be incised to expose the excurrent flow from the colony to entrainment by the current flowing over it (Kott, 1989). Colonies are known to lobulate and to move and space themselves evenly but close to one another (Ryland et al., 1984). Zooids are around the outside of the central cavity where they are embedded in the relatively tough, firm test that is penetrated by narrow cloacal canals at thoracic level. Primary cloacal spaces are post-abdominal and connect with the central cavity beneath the cloacal aperture. In the vicinity of the zooids, colonies are divided into 4 layers of more or less equal thickness viz. the surface layer of test (including the superficial bladder cell layer) in which the anterior parts of the thoraces are embedded, the zooid layer traversed by a network of narrow canals, the posterior abdominal cloacal

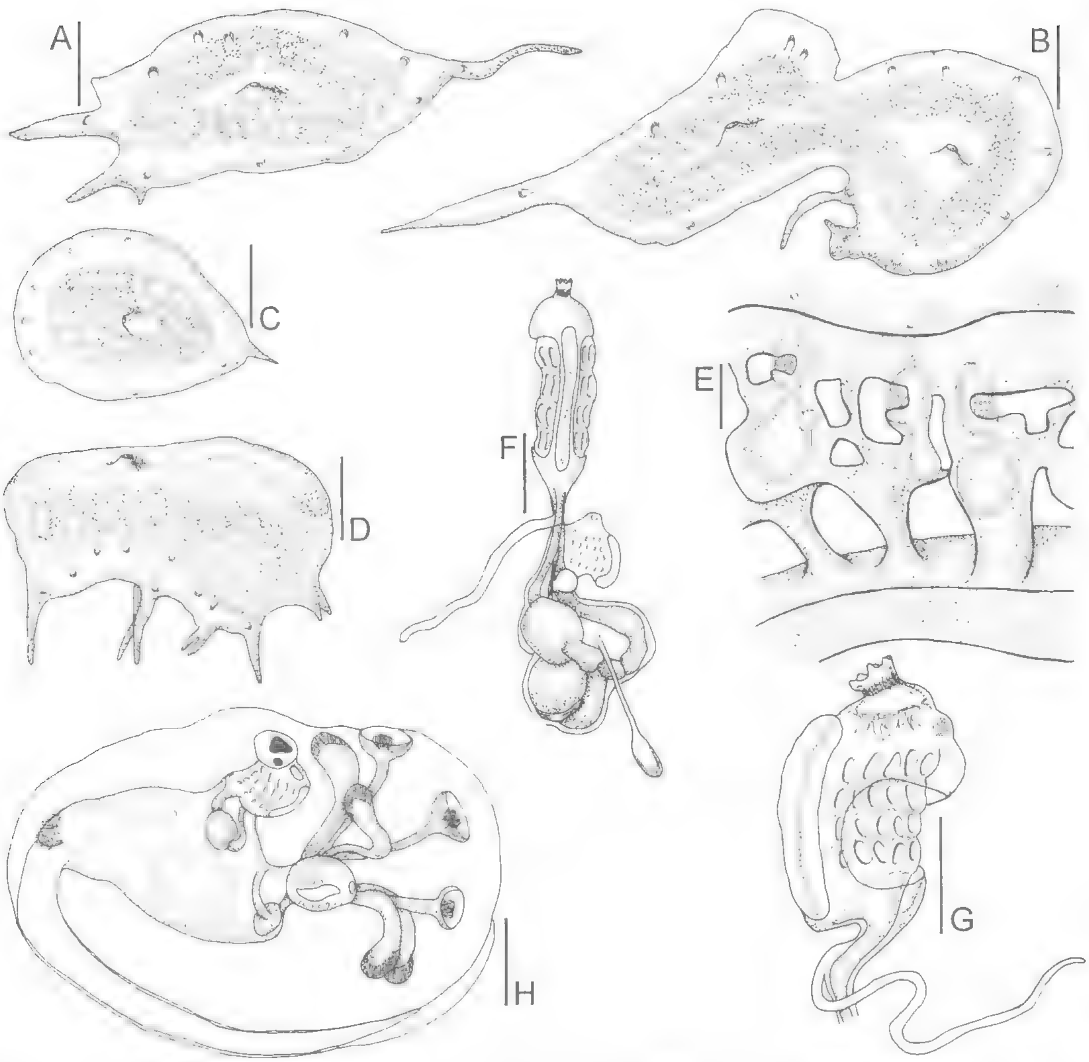


FIG. 156. *Diplosoma virens* (after Kott 1980:A–C, E–G, QM G12484; D, QM G12485; H, QM G9937) — A–C, colonies from above; D, lateral view showing terminal ampullae of test vessels, protuberant common cloacal apertures and dark green around zooids where common cloacal cavities accommodate symbionts; E, semi-diagrammatic vertical section through colony; F, zooid in vegetative phase; G, thorax; H, larva with developing rastrum above base of tail. Scales: A–D, 1.0mm; E, 0.5mm; F–H, 0.2mm.

cavity transversed by strands of test connecting zooid layer to the basal test, and the layer of basal test. The species is in obligate symbiosis with the prokaryote *Prochloron*, which lines the walls of the cloacal cavities and canals.

In life the colonies are paler green in the centre and in the vicinity of the zooids and brighter green around the periphery of the colony where *Prochloron* lining the thoracic as well as the posterior abdominal canals is most abundant. In preservative, colonies are yellowish mustard-green, grey or brownish-yellow. Usually they are opaque owing to the *Prochloron* trapped in the complex three-dimensional network of cloacal spaces in the tough fibrous test.

Long stolonic vessels from the abdominal region of zooids extend through the test connectives into the basal test, and out around the periphery of the colony, where their terminal ampullae can be seen.

ZOOIDS. Zooids are difficult to remove from their tough test sheaths. They are small, about

1.0mm long, the thorax and abdomen of about equal length. In preservative they are whitish, with clear yellow stomach and glandular parts of the intestine. Often some brown squamous epithelium can be seen on the abdominal body wall although this fades in preservative.

The branchial siphon is narrow with a pronounced sphincter muscle. A long, fine retractor muscle is free from about halfway down a long oesophageal neck. The atrial aperture is wide exposing most of the branchial sac directly to the cloacal chamber. Five or 6 rounded to oval or elliptical stigmata lined by flat epithelial cells are in each of the 4 rows. Budding from the oesophageal neck produces 2 sets of buds at any one time and contributes to rapid growth rate of the colonies, and probably their frequent lobulation. The abdomen is bent up at right angles to the long axis of the thorax and oesophageal neck. The post pyloric part of the gut is divided into cylindrical duodenum, posterior stomach, and long rectum constricted halfway up the ascending limb where it is surrounded by tubules of the gastro-intestinal gland. The 2 follicles of the testis are beneath the ventrally flexed part of the gut loop with the proximal part of the vas deferens hooked around between them.

Embryos are found in the basal test of colonies collected in October (from Darwin), March (from Heron I.) and June (from Lizard I.). The larval trunk is up to 1.5mm long, with the tail wound about halfway around it. A rastrum develops above the point of insertion of the tail. Two to 4 pairs of ectodermal ampullae are on each side of the usual 3 median adhesive organs. Larvae of specimens from Lizard I. have 4–8 adhesive organs. One blastozooid is at the anterior end of the trunk. Mature larvae have a deep division separating the oozooid from blastozooid and adhesive array.

REMARKS. Although colony size and number of larval lateral ampullae and adhesive organs is variable, the species has characteristic tough fibrous cushion-like green colonies, cloacal systems (with a network of narrow canals in the upper half of the colony, and extensive posterior abdominal cavities crossed by test connectives from the upper zooid-containing layer), a retractor muscle from at least halfway down the oesophageal neck, and a large larval trunk.

Diplosoma pavonia Monniot & Monniot, 1987 with 7 (rather than 3) larval adhesive organs, is identical with the present species. It appears, therefore, that more than one population has more than 3 and up to 8 adhesive organs (see also Lizard I. populations of the present species: Kott, 1982a). This phenomenom probably reflects some, but not complete, isolation. Monniot (1994) suggested that the Solomon Is populations (*D. pavonia*) are distinguished from *D. virens* by their biochemistry — being more acid. This is unlikely. The pH (down to 2) of didemnid colonies is generated by lysis of bladder cells (Parry, 1984b). It is unlikely that one species can be said to be more acid than the other — even if in an unbuffered medium — as the amount of acid generated is a result of the number of cells that are lysed and its dilution. Differences in the larvae are also invoked to justify the erection of *D. pavonia* as distinct from the present species. However, neither oozooid nor blastozooid are well developed and the rastrum does not appear to have begun its development in larvae examined from the Solomon Is. Other characters are within the range of *D. virens*.

D. matie Monniot & Monniot, 1987, from French Polynesia, is a thin investing colony with a large posterior abdominal cloacal cavity traversed by test connectives between the surface zooid-bearing layer and the base of the colony as in *D. virens*. Zooids, with 2 male follicles and the retractor projecting from at least halfway down the long oesophageal neck, also are like the zooids of *D. virens*. Monniot & Monniot (1987) report it to have symbiotic algae cells (? *Prochloron*), but do not record their location — probably in the cloacal cavity. The colour, which Monniot & Monniot (1987) invoked to distinguish *D. matie* from both *D. pavonia* and *D. simile*, does not provide a reliable distinction. Nevertheless, it does have real distinctions from *D. simile* and it is *D. virens*, and not *D. simile*, which is most closely related to *D. matie*. *D. simile* is distinguished from both *D. matie* and *D. virens* by its smaller larval trunk, the retractor muscle protruding from the posterior end of the thorax rather than from the middle to base of the oesophagus and the extensive thoracic rather than posterior abdominal cloacal cavity. The larva (Monniot & Monniot, 1987, fig. 30G) of *D. matie* is not well developed, the rastrum is rudimentary and neither oozooid nor blastozooid are well formed. However, other larval organs are developed. It has a large trunk (0.85mm long), 5 –12 adhesive organs and 5 or 6 pairs of ectodermal ampullae. The greater number of ectodermal ampullae provide the only real distinction from *D. virens*, although in view of the variations in *D. virens* larvae, this distinction is

not very conclusive. *D. virens* has a larval trunk of 1–1.5mm, a variable number of adhesive organs, but only 2–4 pairs of ectodermal ampullae (Philippines: Kott, 1982a). Variations in the size and numbers of ectodermal ampullae in larvae of *D. matie* are outside the range recorded for *D. virens*, but they may only represent the genetic diversity that could be expected in a species with partially isolated populations from the central Pacific to the Indian Ocean; and it is possible that this species would be more accurately treated as a synonym of *D. virens*.

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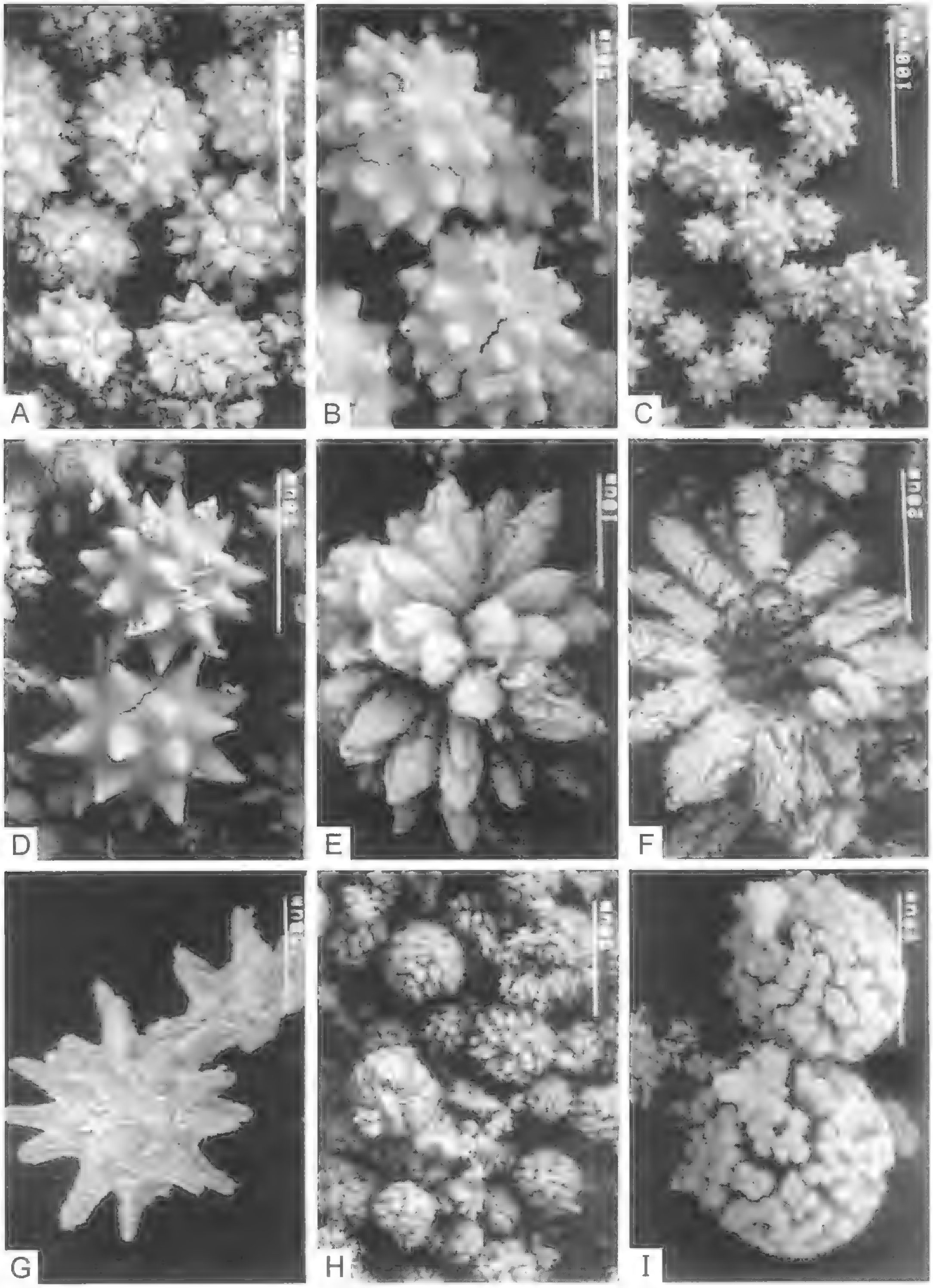


FIG. 157. A, *Atriolum robustum* (QM G305675); B, *A. lilium* (QM GH2385); C, *A. tubiporum* (QM G302885); D, *A. bucinum* (QM G304670); E,F, *A. marinense* (QM G301616) showing hollow spicule; G, *A. eversum* (WAM 366.80); H, *Leptoclinides comitus* (SAM E2614); I, *L. volvus* (SAM E1034).

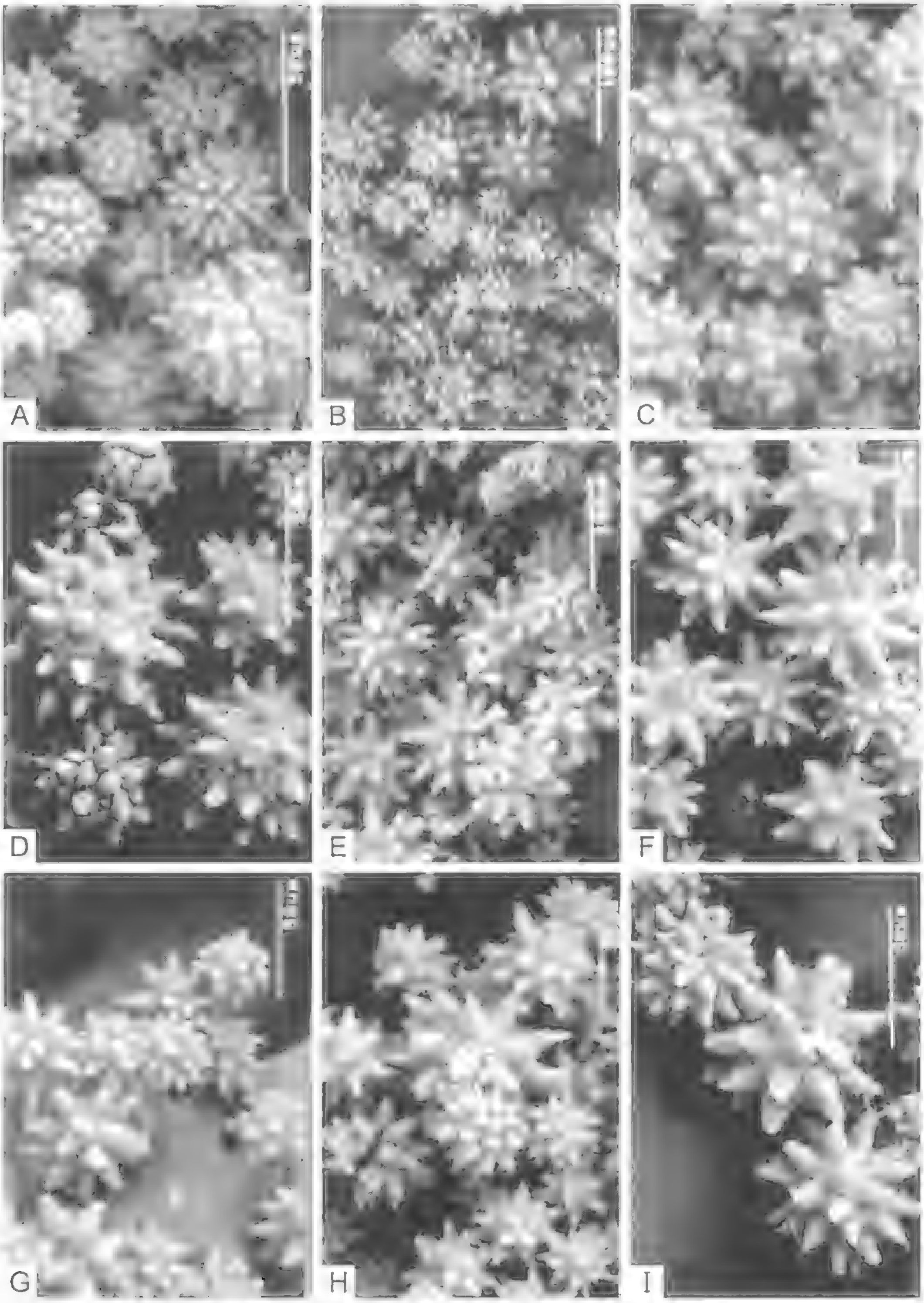


FIG. 158. A, *Leptoclinides carduus* (QM G308154); B, *L. rufus* (QM G301757); C, *L. confirmatus* (SAM E2619); D, *L. umbrosus* (QM G308429); E, *L. erinaceus* (WAM 128.93); F, *L. magnistellus* (AM Y1481); G, *L. albamaculatus* (QM G308291); H, *L. cuspidatus* (ZMA TU440.2); I, *L. cavernosus* (QM G308247).

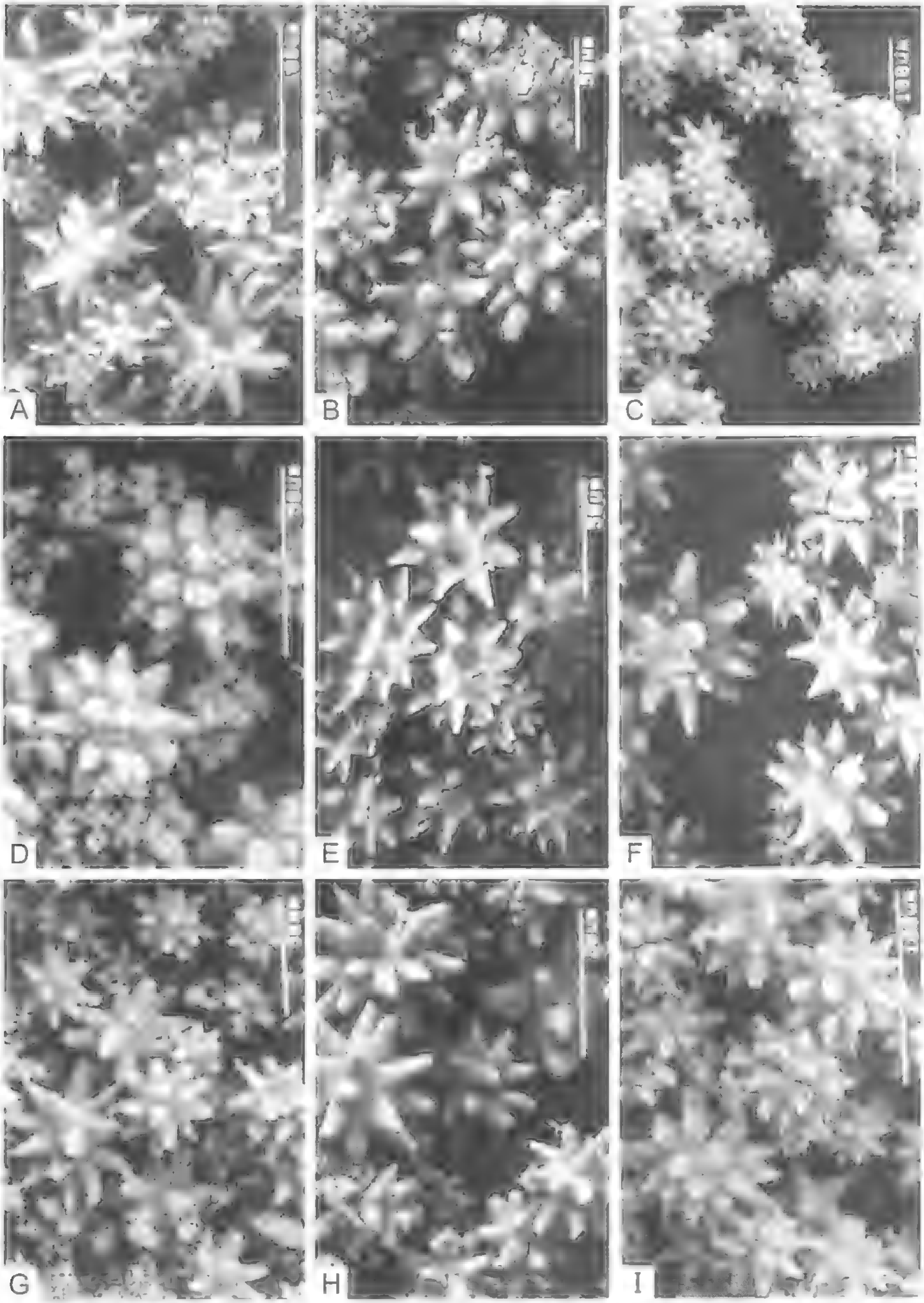


FIG. 159. A, *Leptoclinides imperfectus* (QM G302883); B, *L. variegatus* (SAM E2697); C, *L. coelenteratus* (AM Y1343); D, *L. longicollis* (QM G300898); E, *L. brandi* (QM G308104); F, *L. aciculus* (QM G303827); G, *L. maculatus* (SAM E2659); H, *L. exiguus* (MV F68745); I, *L. placidus* (QM GH372).

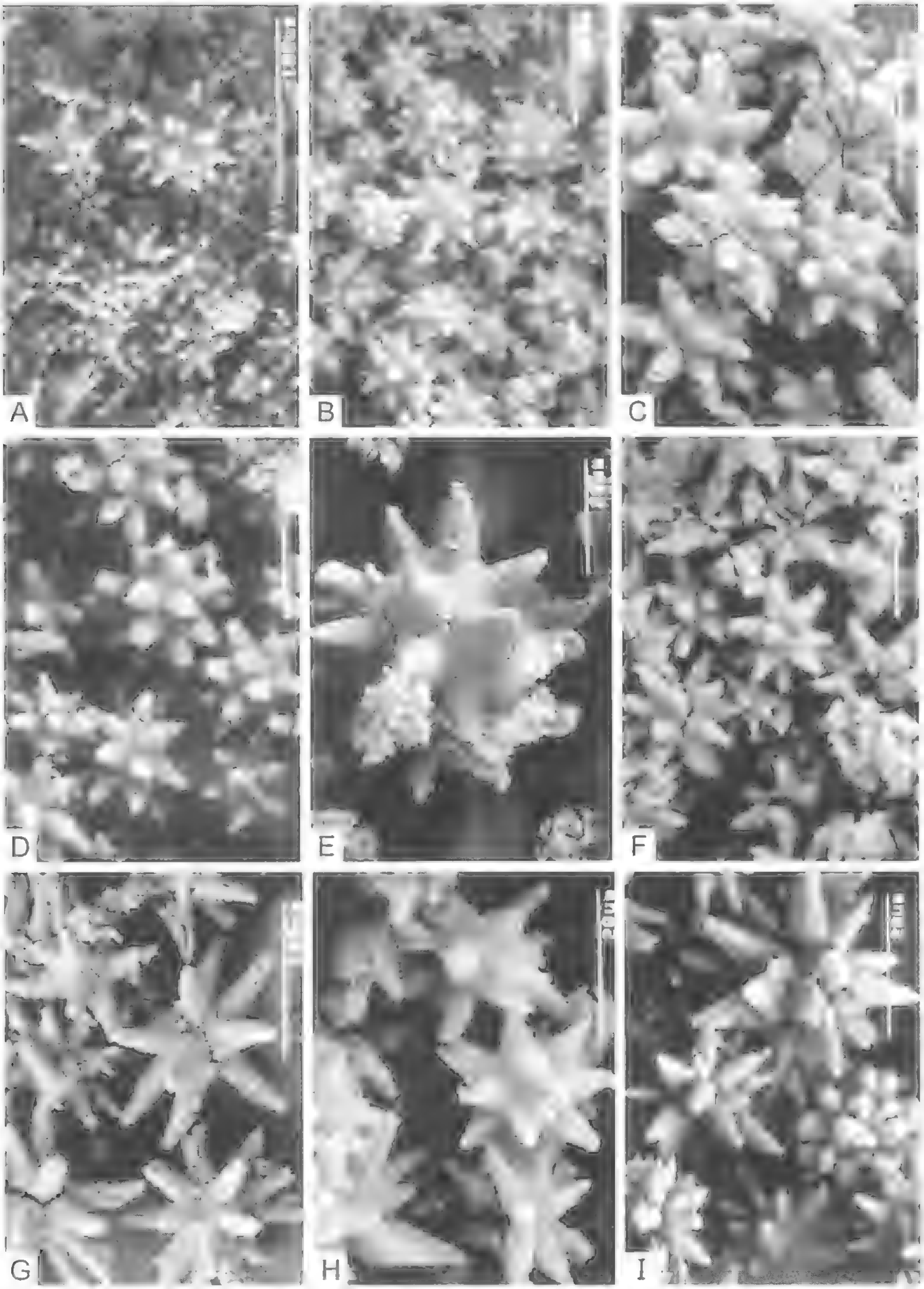


FIG. 160. A, *Leptoclinides constellatus* (QM GH5420); B, *L. seminudus* (SAM E2671); C, *L. rigidus* (QM GH5371); D, *L. compactus* (SAM E2635); E, *L. sulawesi* (QM G308493); F, *L. lissus* (AM G13449); G, *L. caelestis* (WAM 794.88); H, *L. echinus* (QM GH2121); I, *L. levitatus* (QM G308700).

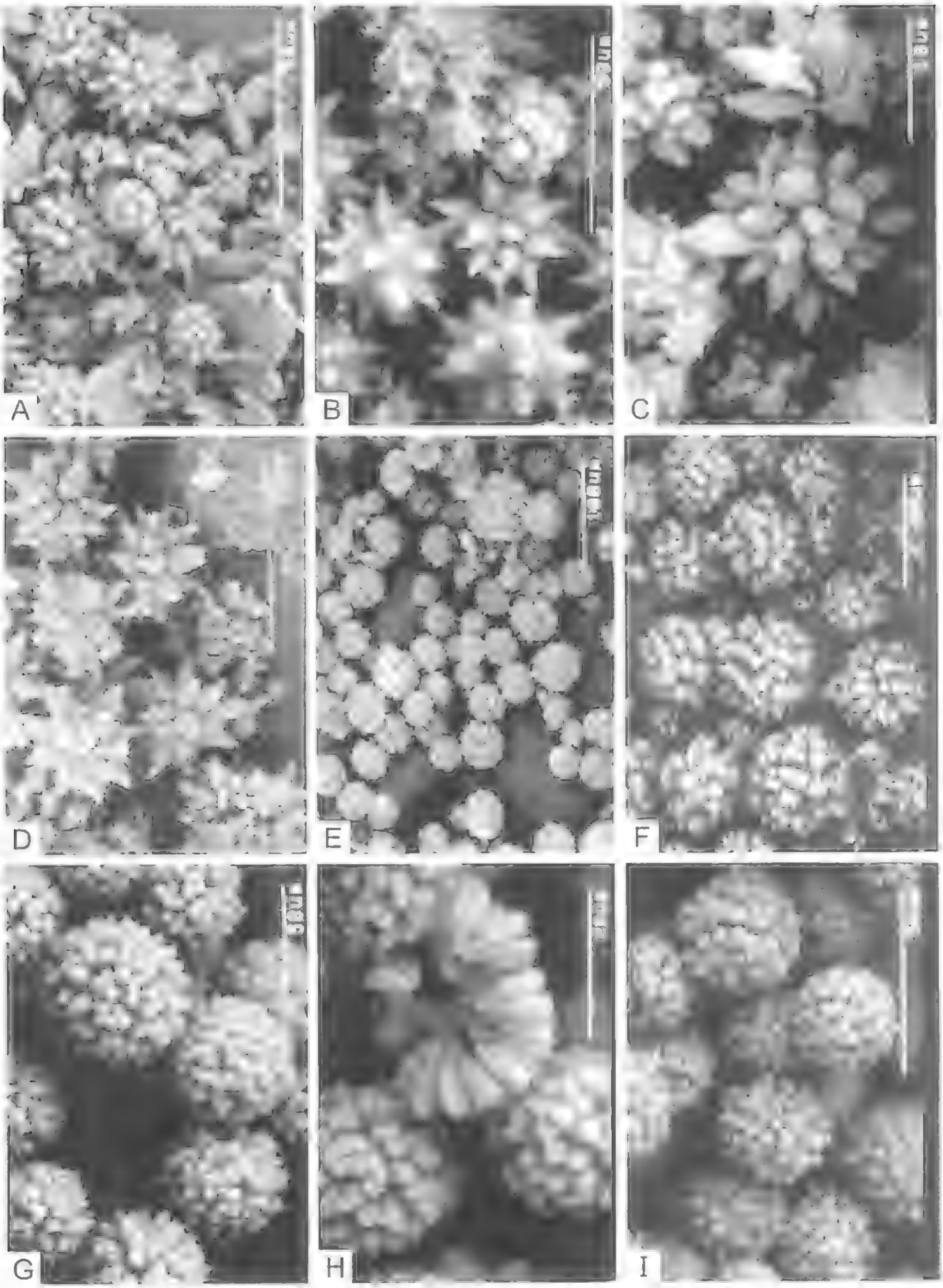


FIG. 161. A, *Leptoclinides dubius* (QM G308239); B, *L. durus* (QM G3023507); C, *L. multilobatus* (QM GH1317); D, *L. kingi* (QM GH5369); E, *Polysyncraton flammeum* (QM G308461); F, *P. discoides* (SAM E2623); G,H, *P. circulum* (QM G308191 showing hollow spicules); I, *P. scorteum* (SAM E2629).

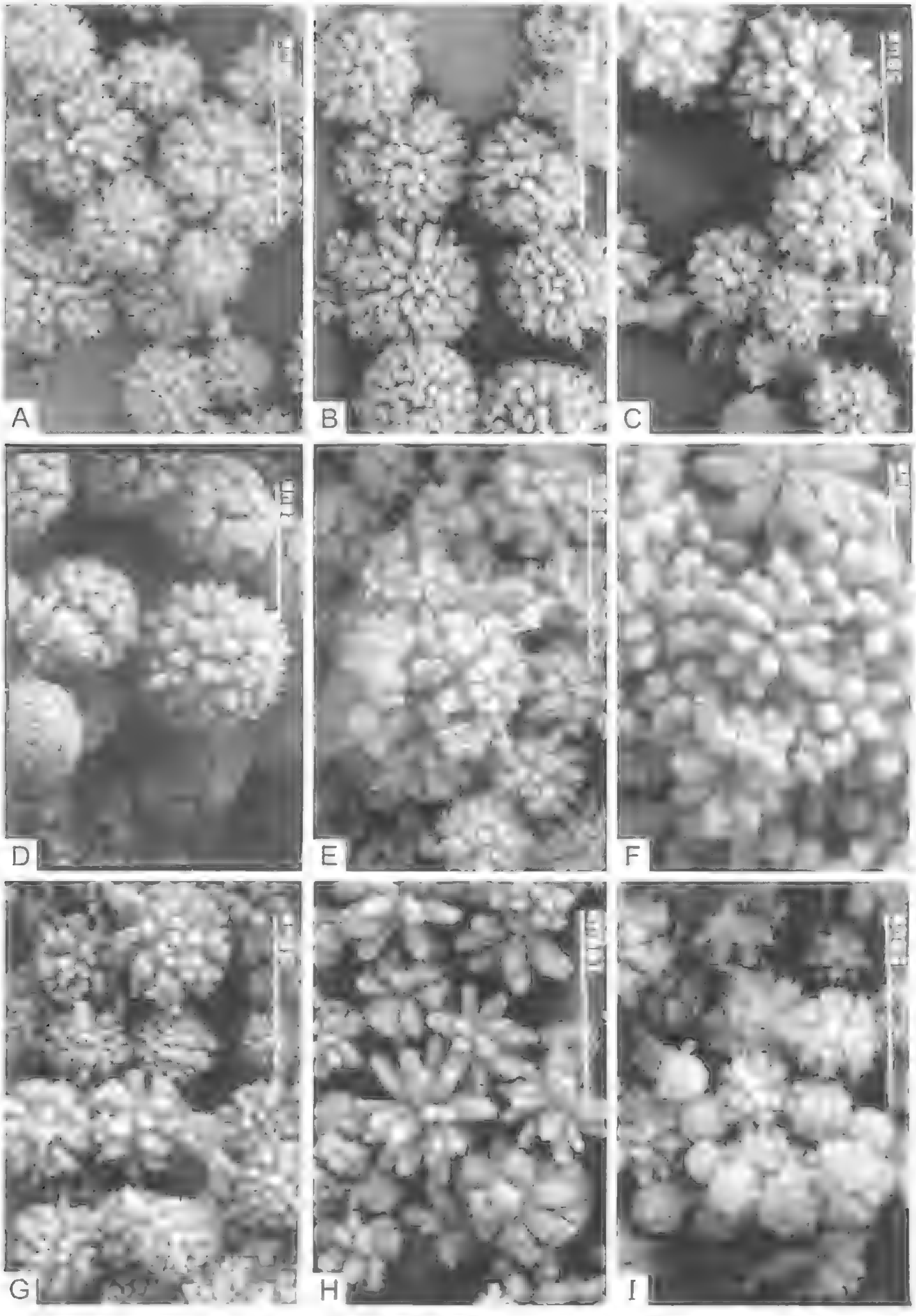


FIG. 162. A, *Polysyncraton pulchrum* (WAM 137.93); B, *P. meandratum* (QM G308217); C, *P. purou* (QM G308231); D, *P. dentatum* (SAM E2677); E, *P. dromide* (QM G301568); F, *P. orbiculum* (AM Y1484); G, *P. rugosum* (QM G305554); H, *P. pontoniae* (QM G308019); I, *P. magnetae* (QM G301538).

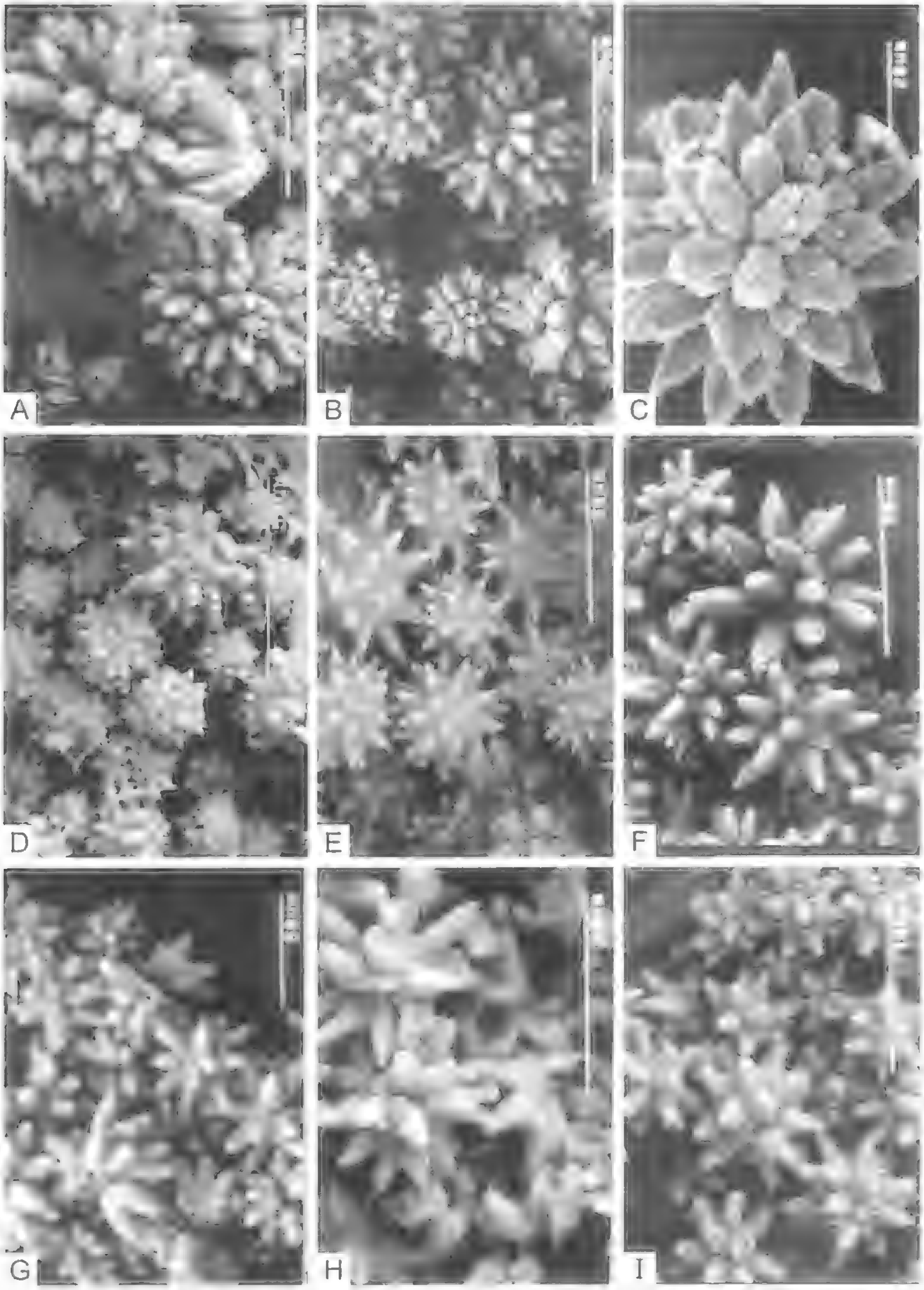


FIG. 163. A, *Polysyncraton robustum* (AM Y2312); B, *P. palliolum* (QM G300988); C, *P. regulum* (QM G308474); D, *P. multiforme* (QM G304641); E, *P. arafurensis* (WAM 108.93); F, *P. echinatum* (QM G300993); G, *P. glaucum* (QM G305628); H, *P. pseudorugosum* (QM G308347); I, *P. lodix* (QM GH5751).

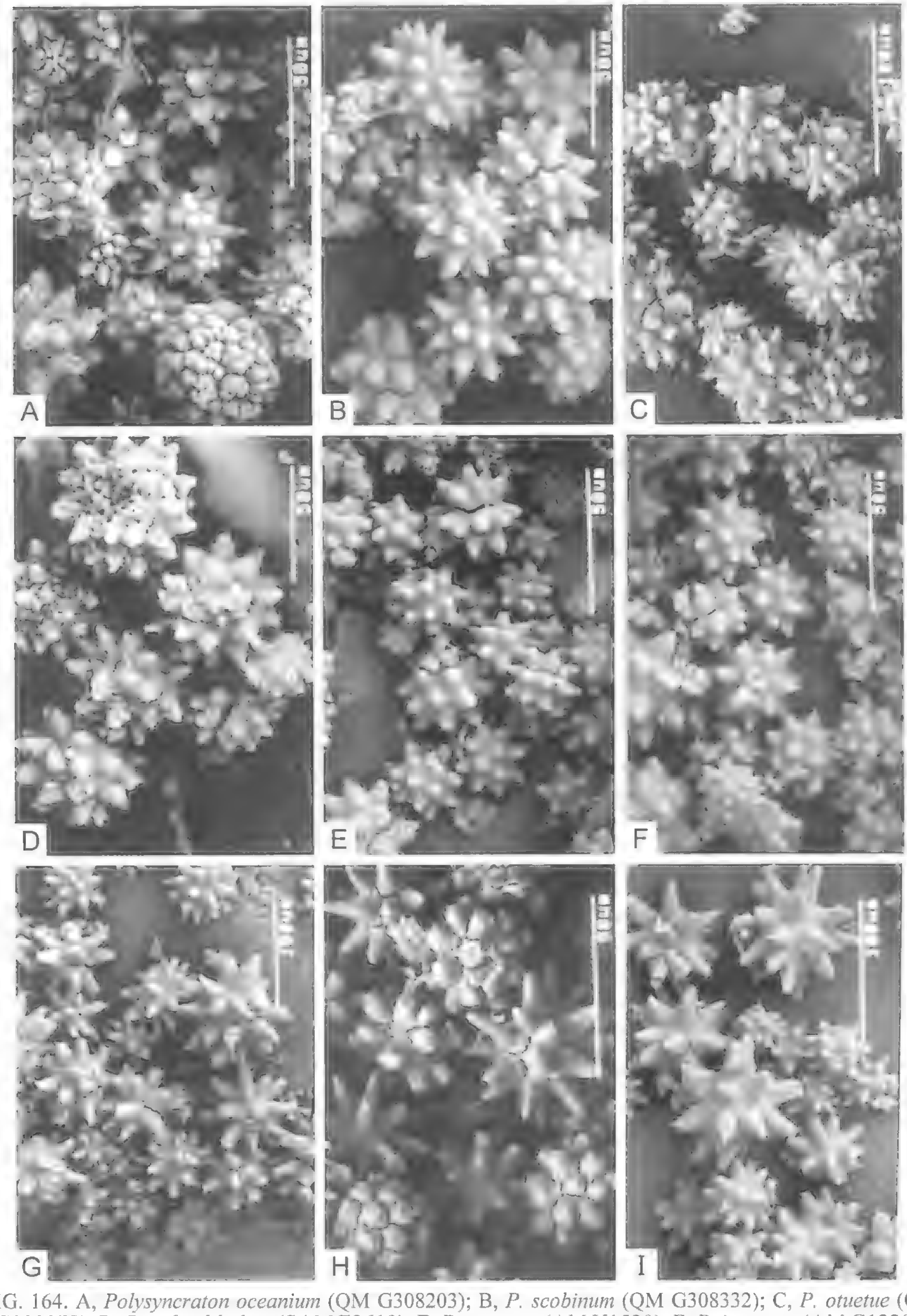


FIG. 164. A, *Polysyncraton oceanium* (QM G308203); B, *P. scobinum* (QM G308332); C, *P. otuetue* (QM G308378); D, *P. infundibulum* (SAM E2610); E, *P. papyrus* (AM Y1520); F, *P. jugosum* (AM G12205); G, *P. tegetum* (SAM E2698); H, *P. millepore* (QM G302945); I, *P. tasmanense* (AM Y1541).

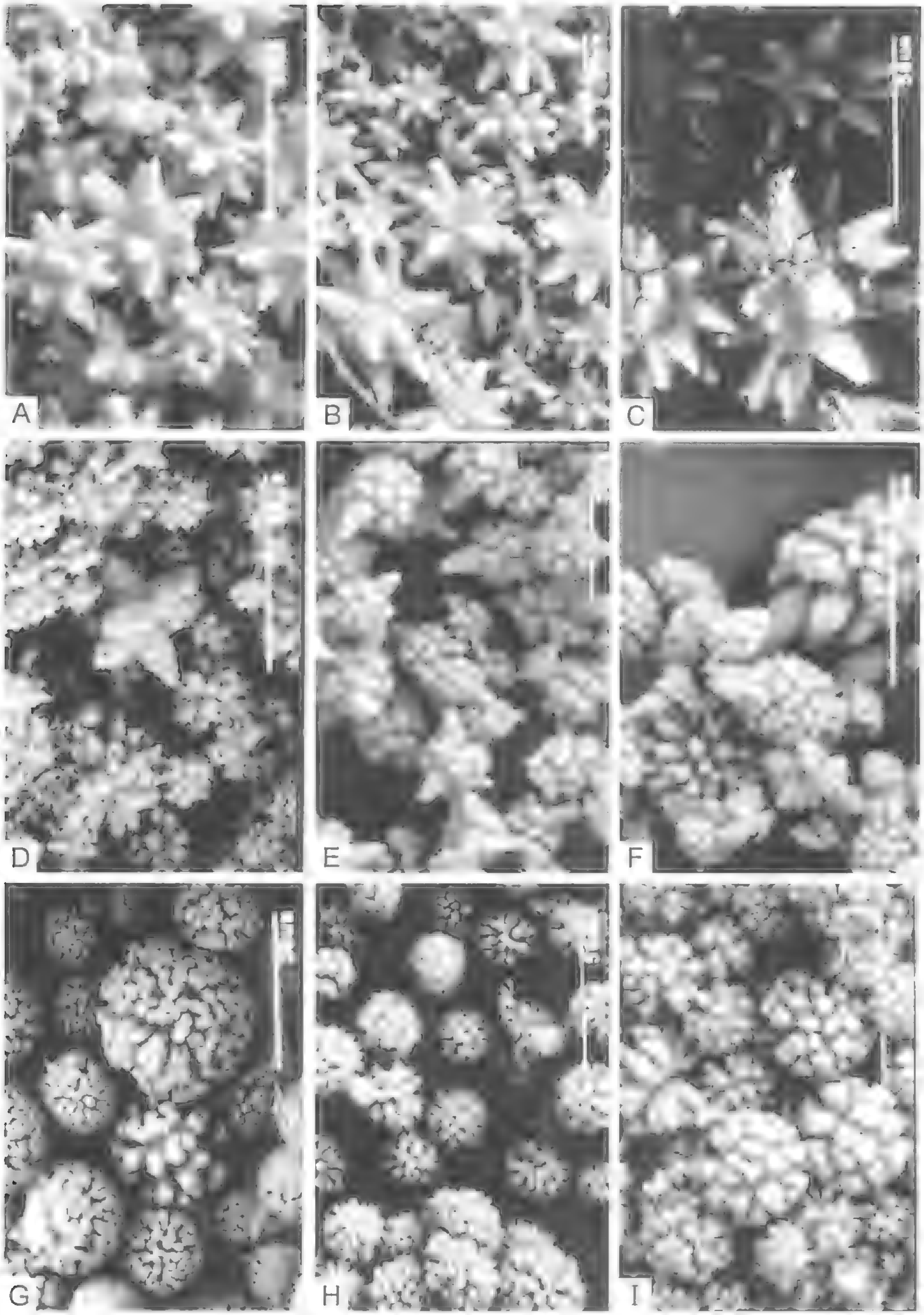


FIG. 165. A, *Polysyncraton rubitapum* (QM GH1330); B, *P. sideris* (AM Y1487); C, *P. rica* (QM GH5426); D, *P. tenuicutis* (WAM 390.75). E,F, *Didemnum uturoa* (QM G301956, G308287); G, *D. precocinum* (WAM 521.92); H, *D. albopunctatum* (QM G308031); I, *D. oblitum* (QM G308380).

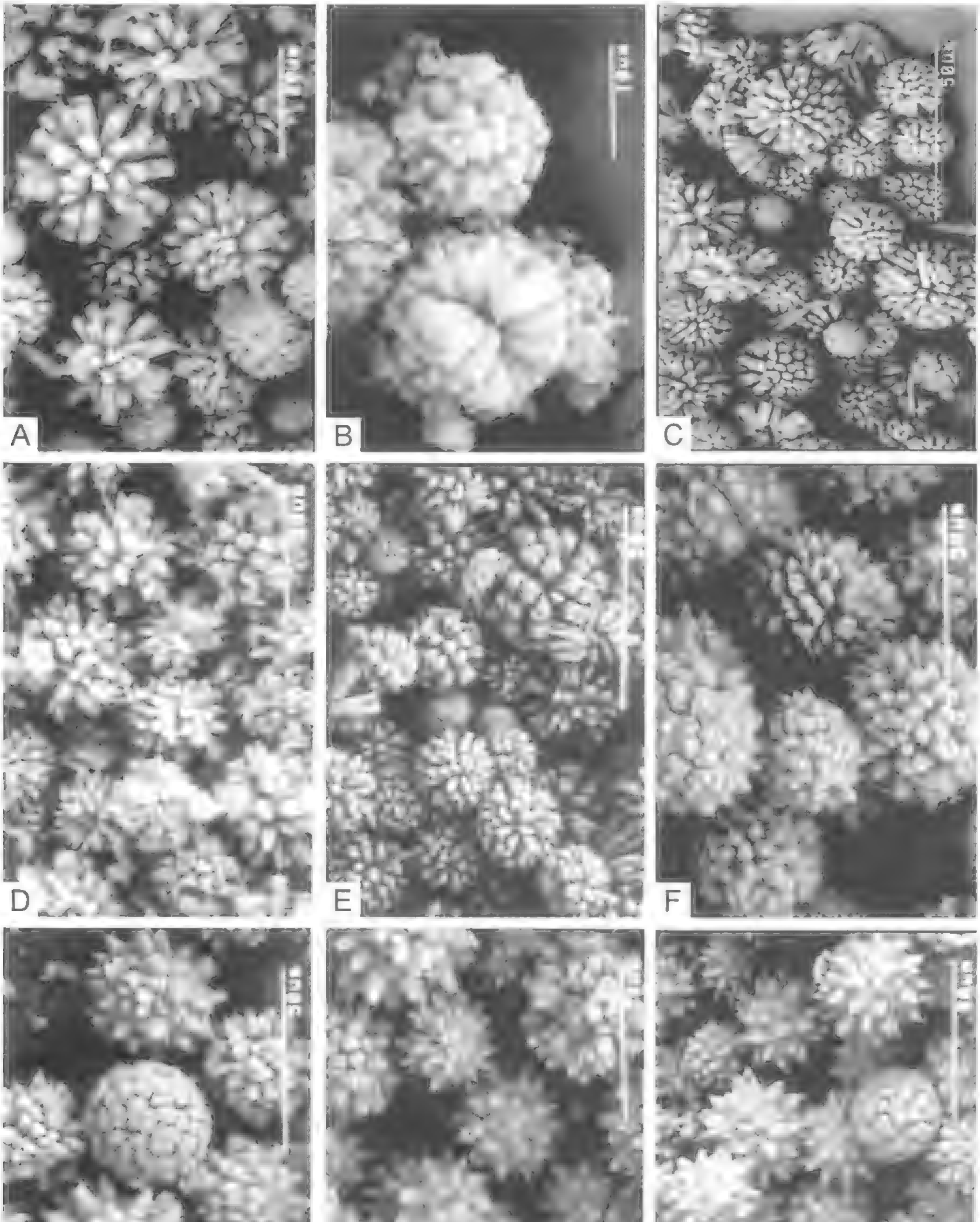


FIG. 166. A, *Didemnum fragile* (QM G308401); B, *D. flavoviride* (QM GH3477); C, *D. molle* (QM G308534); D, *D. hiopaa* (QM G308308); E, *D. parancium* (QM GH5353); F, *D. arancium* (QM G308218); G, *D. chartaceum* (QM G308266); H, *D. levitas* (QM G308224); I, *D. multispirale* (QM G302920).

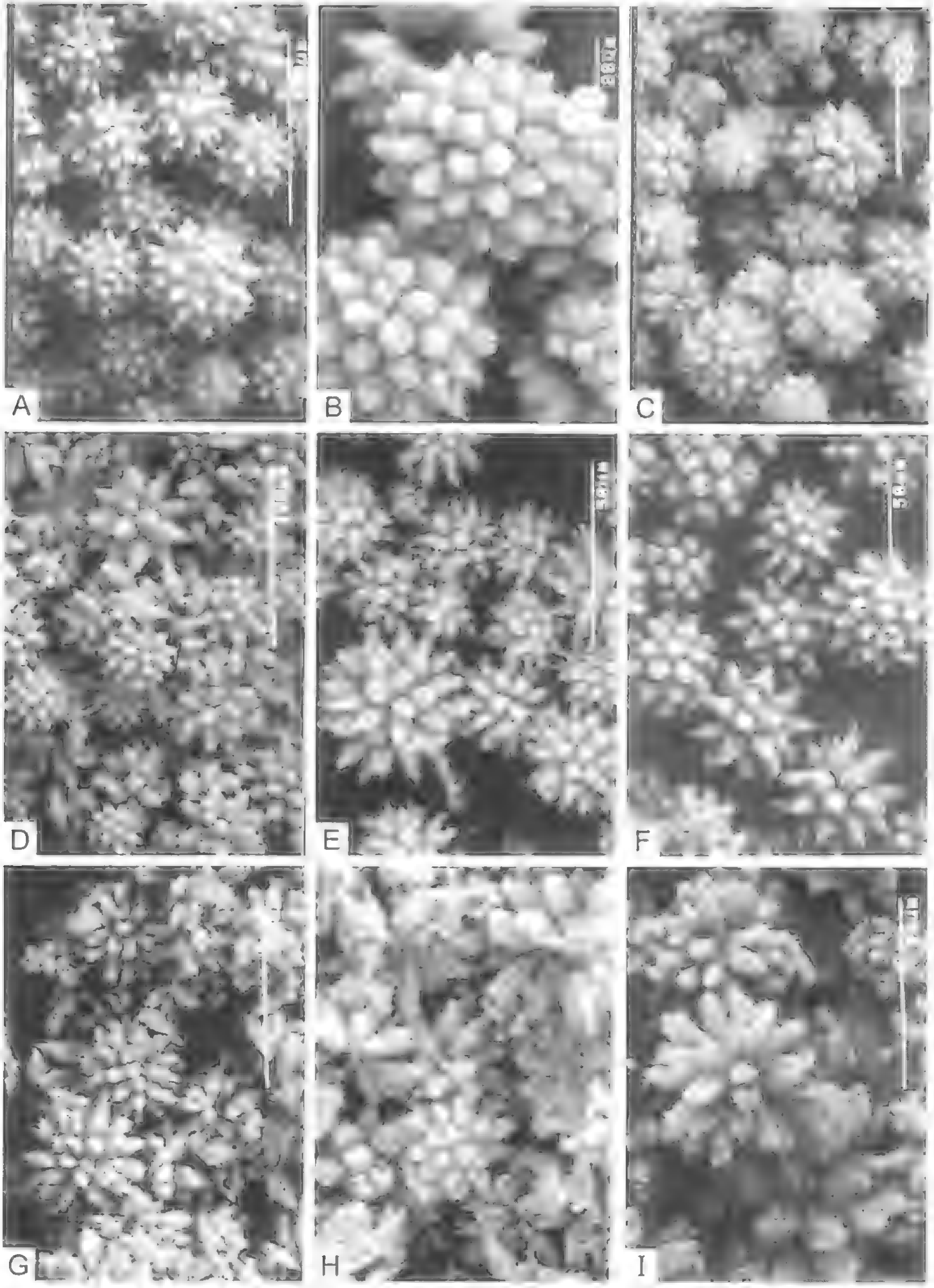


FIG. 167. A, *Didemnum mutabile* (QM G308205); B, *D. lacertosum* (QM G308006); C, *D. ternerratum* (SAM E2653); D, *D. jucundum* (SAM E2693); E, *D. tabulatum* (ZMA TU480.3); F, *D. astrum* (QM G308112); G, *D. jedanense* (QM G308491); H, *D. monile* (SAM E2683); I, *D. theca* (WAM 121.93).

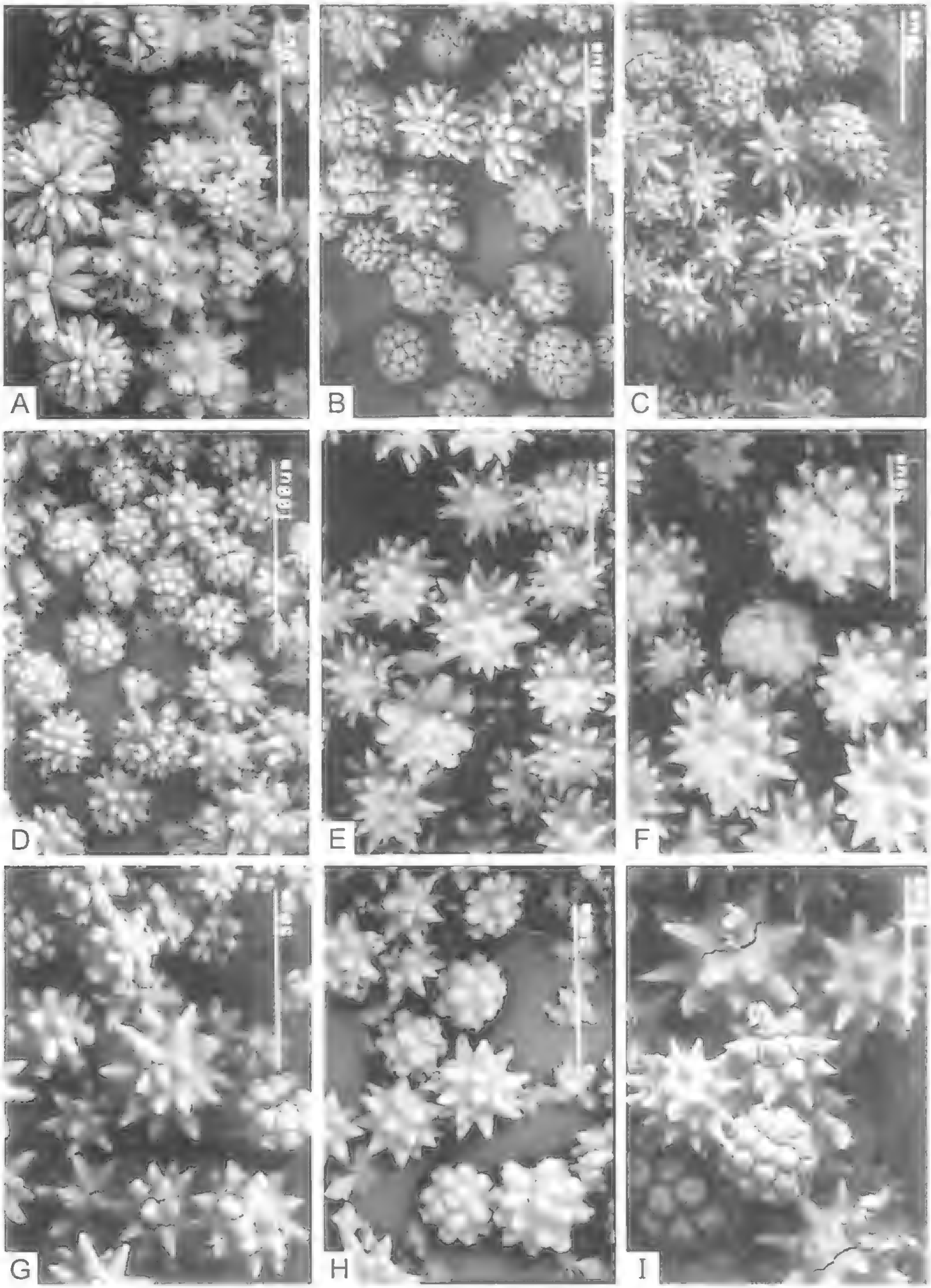


FIG. 168. A, *Didemnum psammatode* (QM G308143); B, *D. poecilomorpha* (QM G302890); C, *D. ossium* (QM G302908); D, *D. moseleyi* (BMNH 1887.2.4.404 holotype); E, *D. inveteratum* (QM G302922); F, *D. bisectatum* (QM G302599); G, *D. bicolor* (QM GH 2410); H, *D. macrosiphonium* (SAM E2658); I, *D. guttatum* (QM G302876).

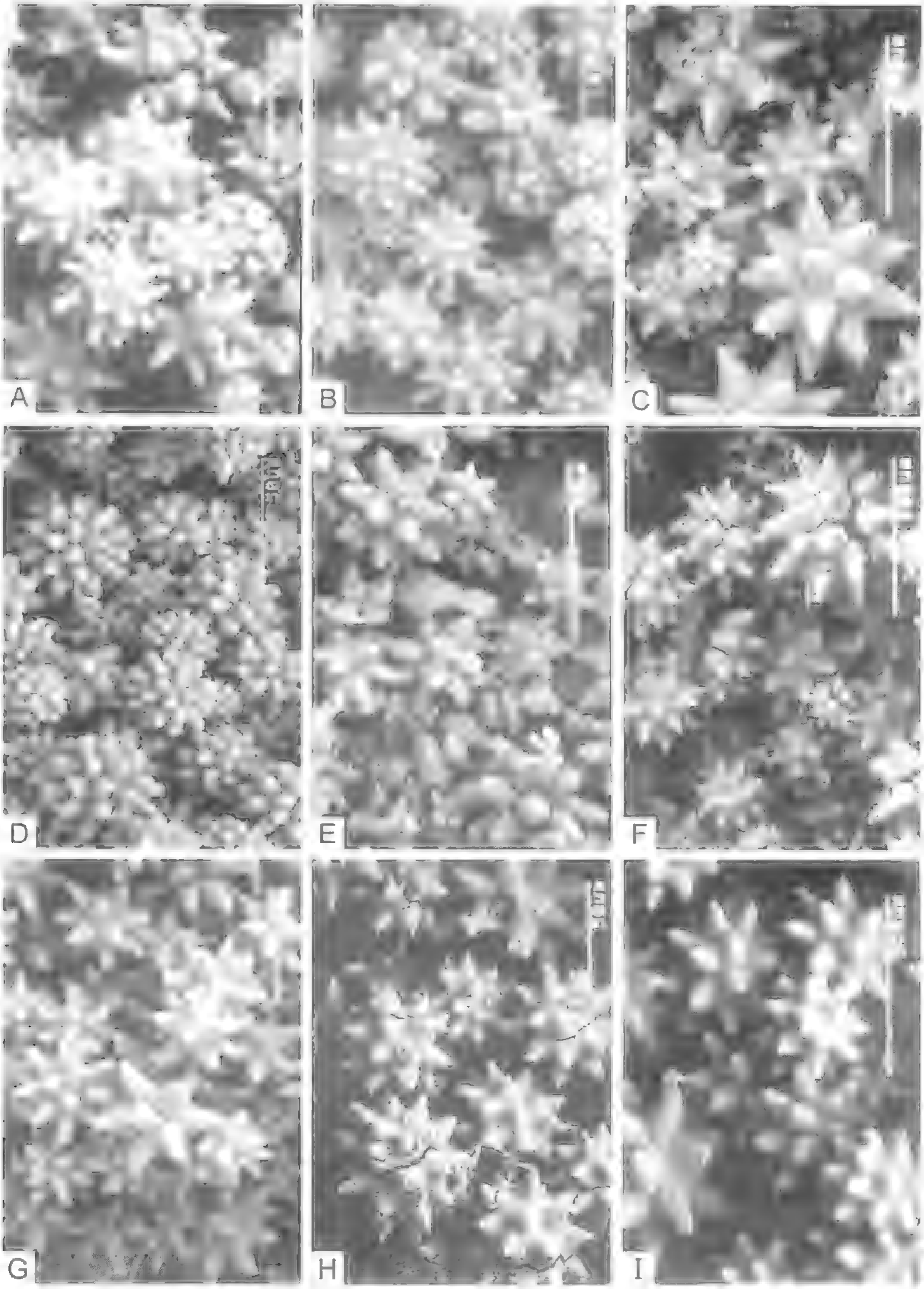


FIG. 169. A, *Didemnum vahatuio* (QM G305373); B, *D. elongatum* (WAM 79.89); C, *D. pellucidum* (SAM E2696); D, *D. vulgare* (SAM E2855); E, *D. spadix* (SAM E2694); F, *D. linatum* (WAM 40.89); G, *D. lissoclinum* (SAM E2665); H, *D. fragum* (AM Y1519); I, *D. patulum* (MV F70207).

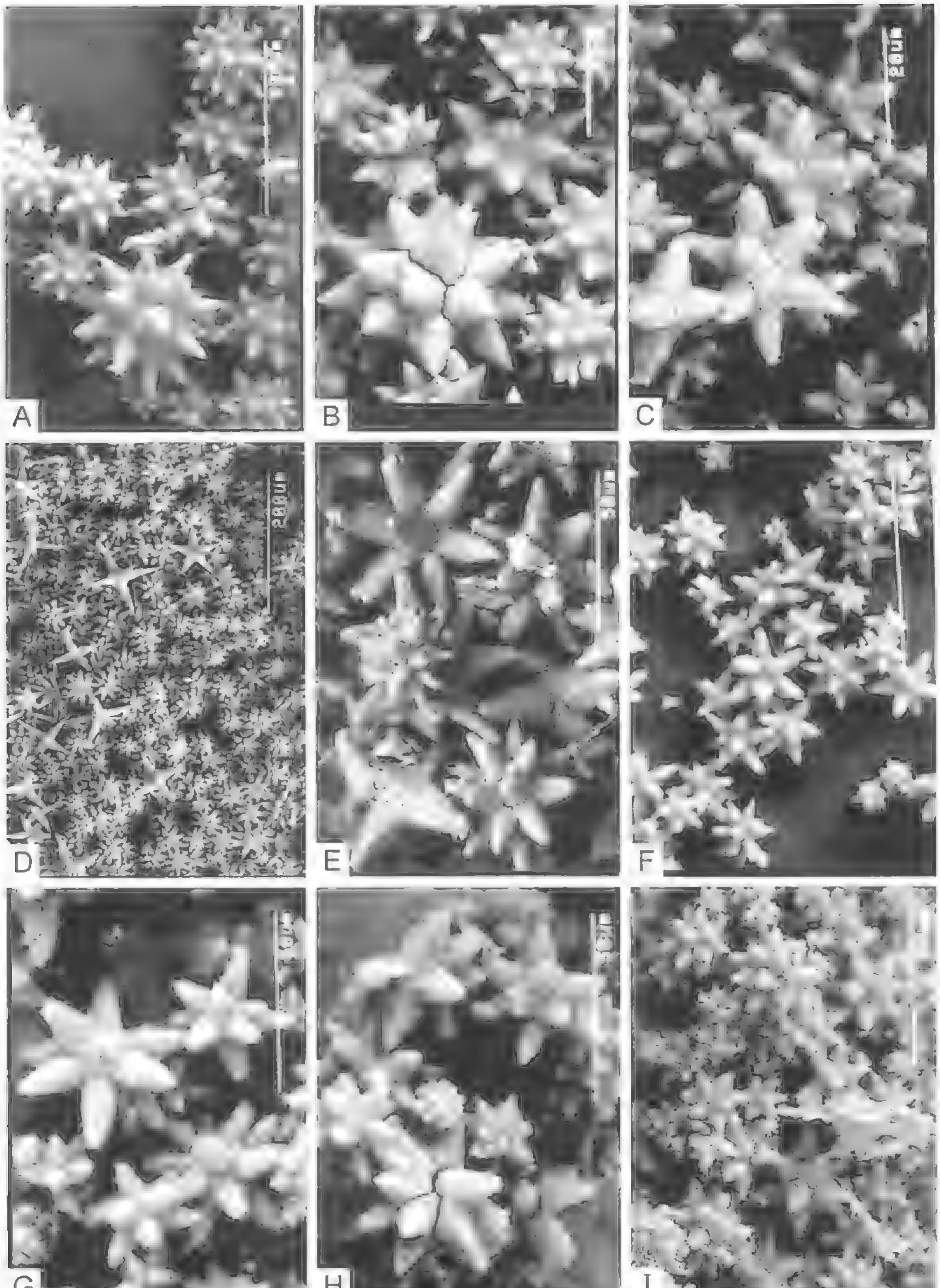


FIG. 170. A, *Didemnum caesium* (QM G308290); B, *D. sucosum* (AM U182); C, *D. incanum* (AM Z5134); D, *D. membranaceum* (QM G308532); E, *D. complexum* (AM Y820); F, *D. perplexum* (QM G302960); G, *D. etiolum* (QM G301528); H, *D. cygnus* (WAM 362.92); I, *D. pecten* (QM 300929).

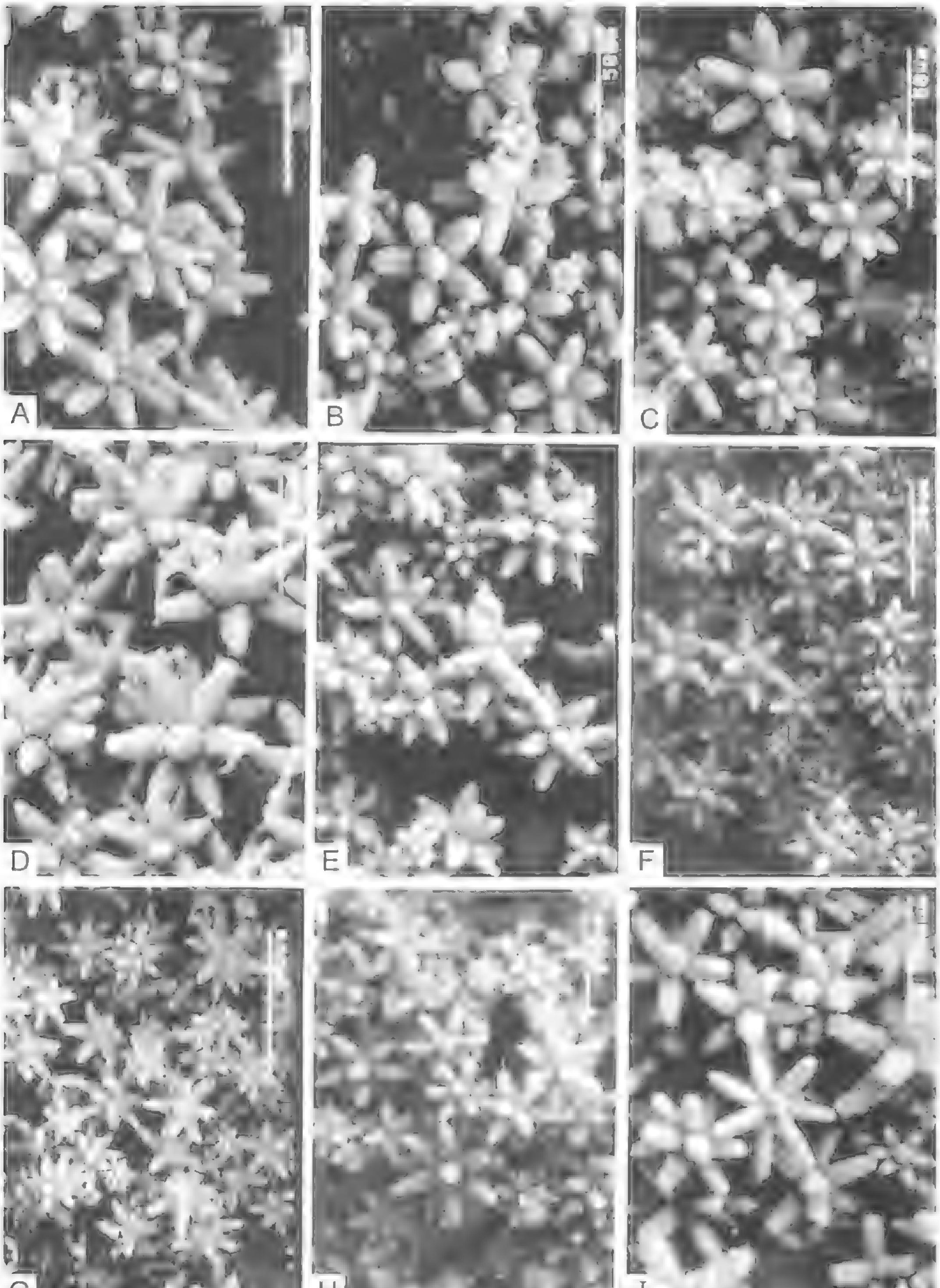


FIG. 171. A, *Didemnum fuscum* (QM G308264); B,C, *D. candidum* (QM G308215, G308202); D, *D. mantile* (QM G302881); E, *D. spongioide* (QM G303640); F, *D. granulatum* (QM GH5379); G, *D. stragulum* (WAM 610.89); H, *D. delectum* (SAM E2674); I, *D. verdantum* (QM GH5358).

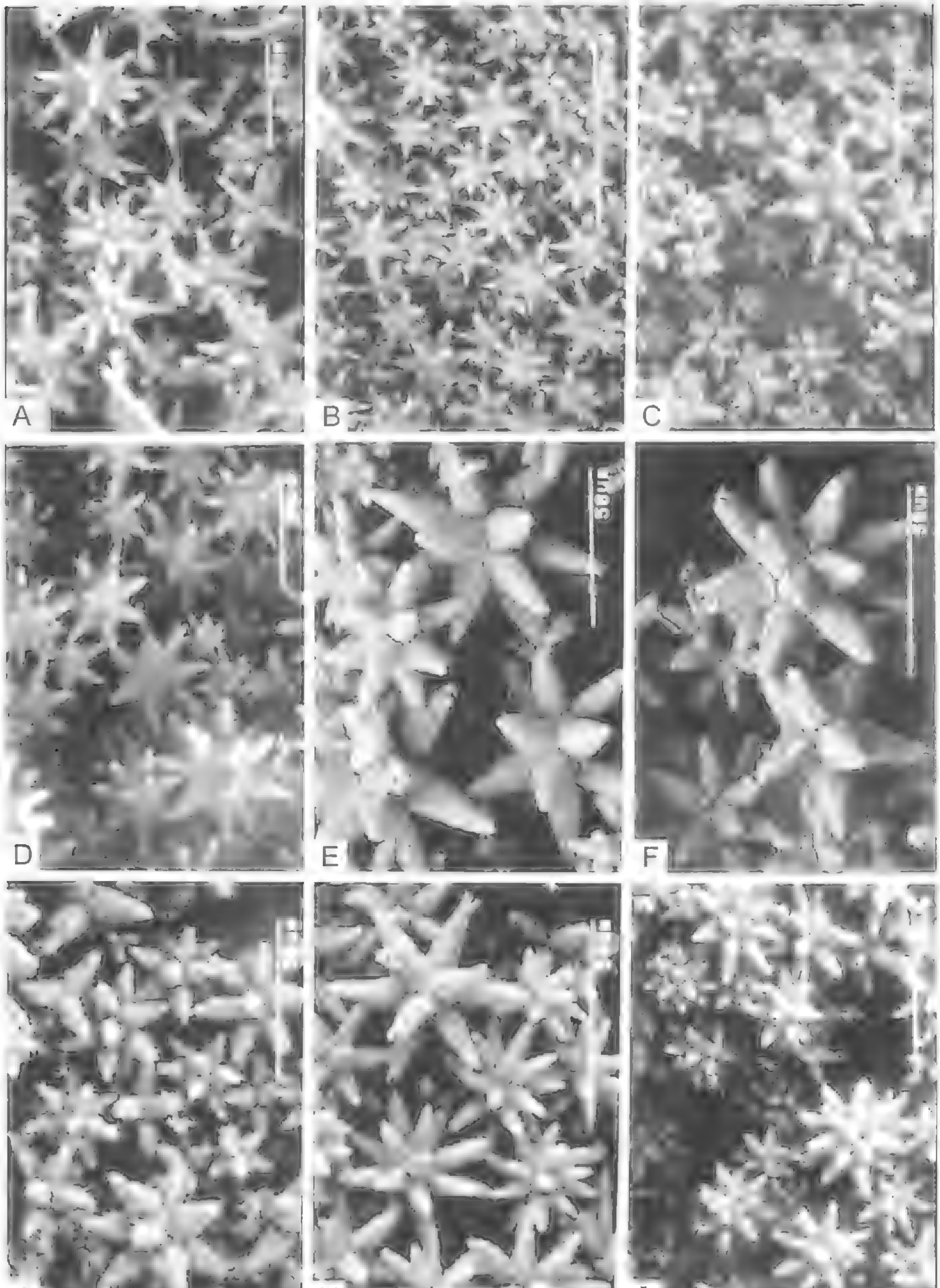


FIG. 172. A, *Didemnum fucatum* (ZMA TU448); B, *D. roberti* (WAM 524.92); C, *D. microthoracium* (SAM E2656); D, *D. herba* (QM G308641); E, *D. grande* (WAM 42.82); F, *D. crescente* (MV F68801); G, *D. viride* (QM G305798); H, *D. clavum* (WAM 103.93); I, *D. via* (QM GH808).

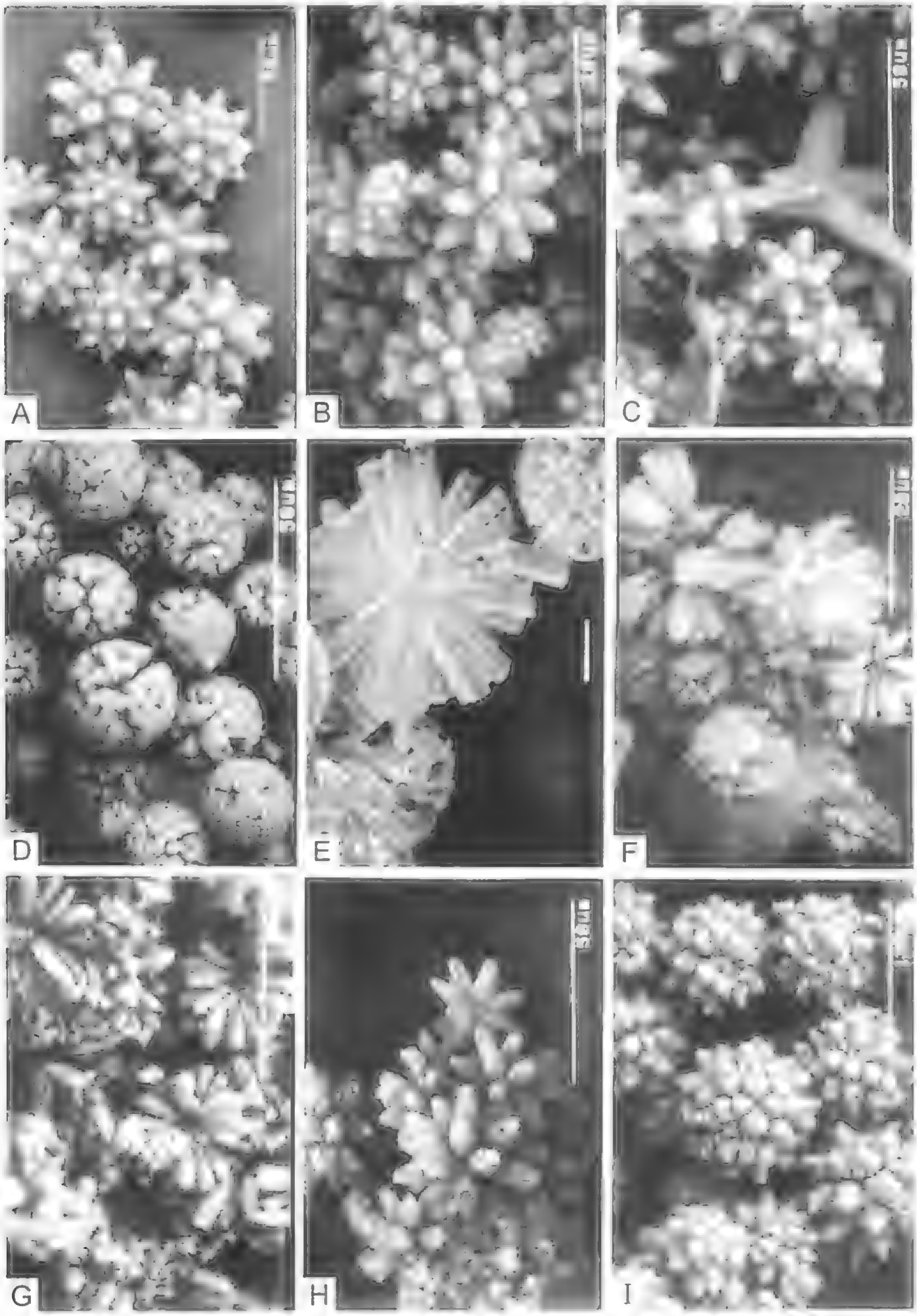


FIG. 173. A, *Didemnum sordidum* (QM GH1836); B, *D. scopi* (QM G308219); C, *D. cuculliferum* (QM G308190); D,E, *Trididemnum miniatum* (ZMA TU441.2, QM G9927 – scale 0.005mm); F, *T. spumosum* (SAM E2616); G, *T. crystallinum* (QM G302608 – scale 0.05mm); H, *T. clinides* (QM G301600); I, *T. areolatum* (QM G308426).

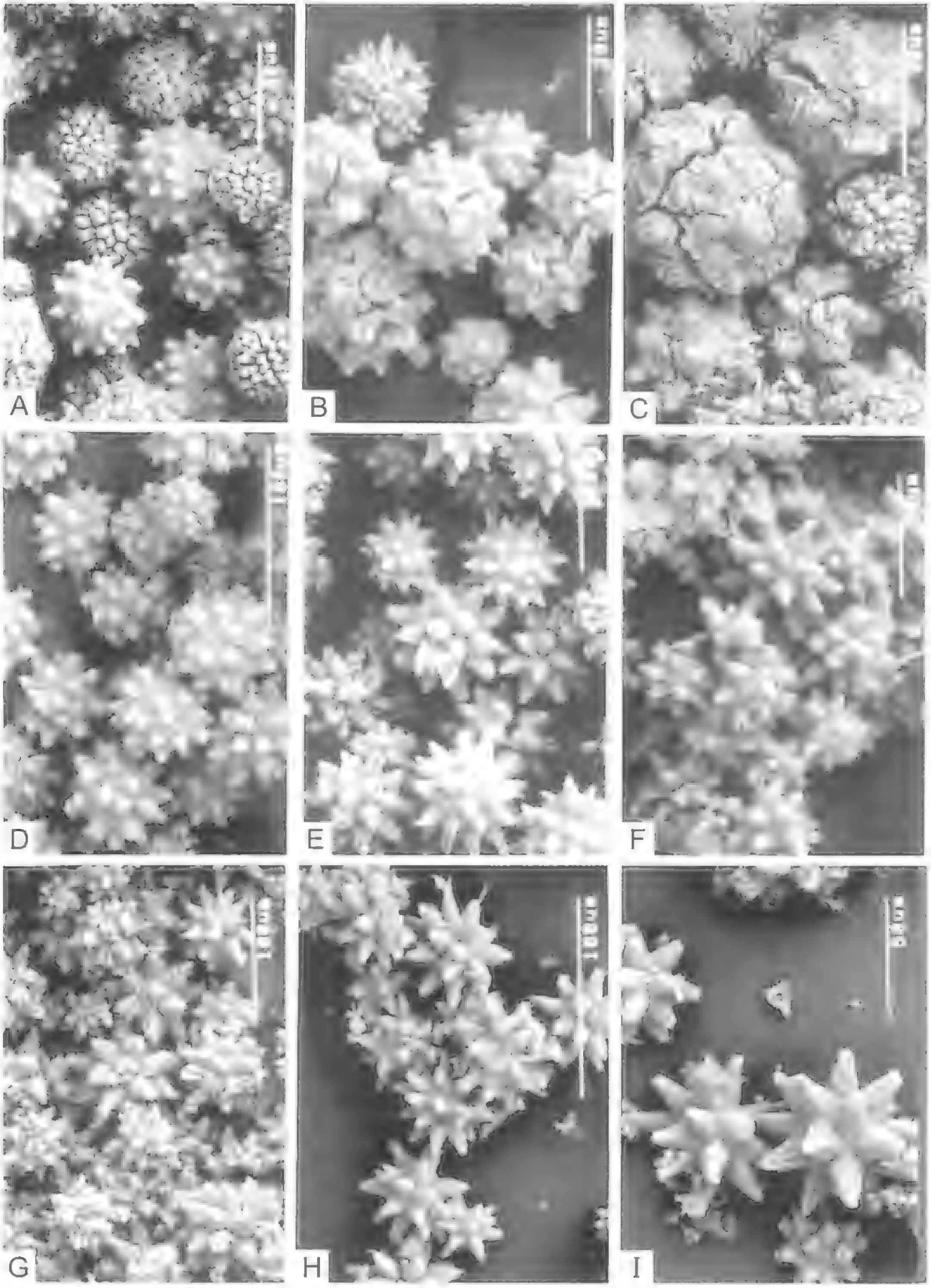


FIG. 174. A, *Trididemnum paracyclops* (QM G12628); B,C, *T. dispersum* (ZMA TU443.1, QM G301780); D, *T. cyclops* (QM G308152); E, *T. nubilum* (QM GH150); F, *T. nobile* (QM GH2371); G, *T. amiculum* (AM Z1681); H, *T. tomarahi* (QM G308327); I, *T. vermiforme* (SAM E2602).

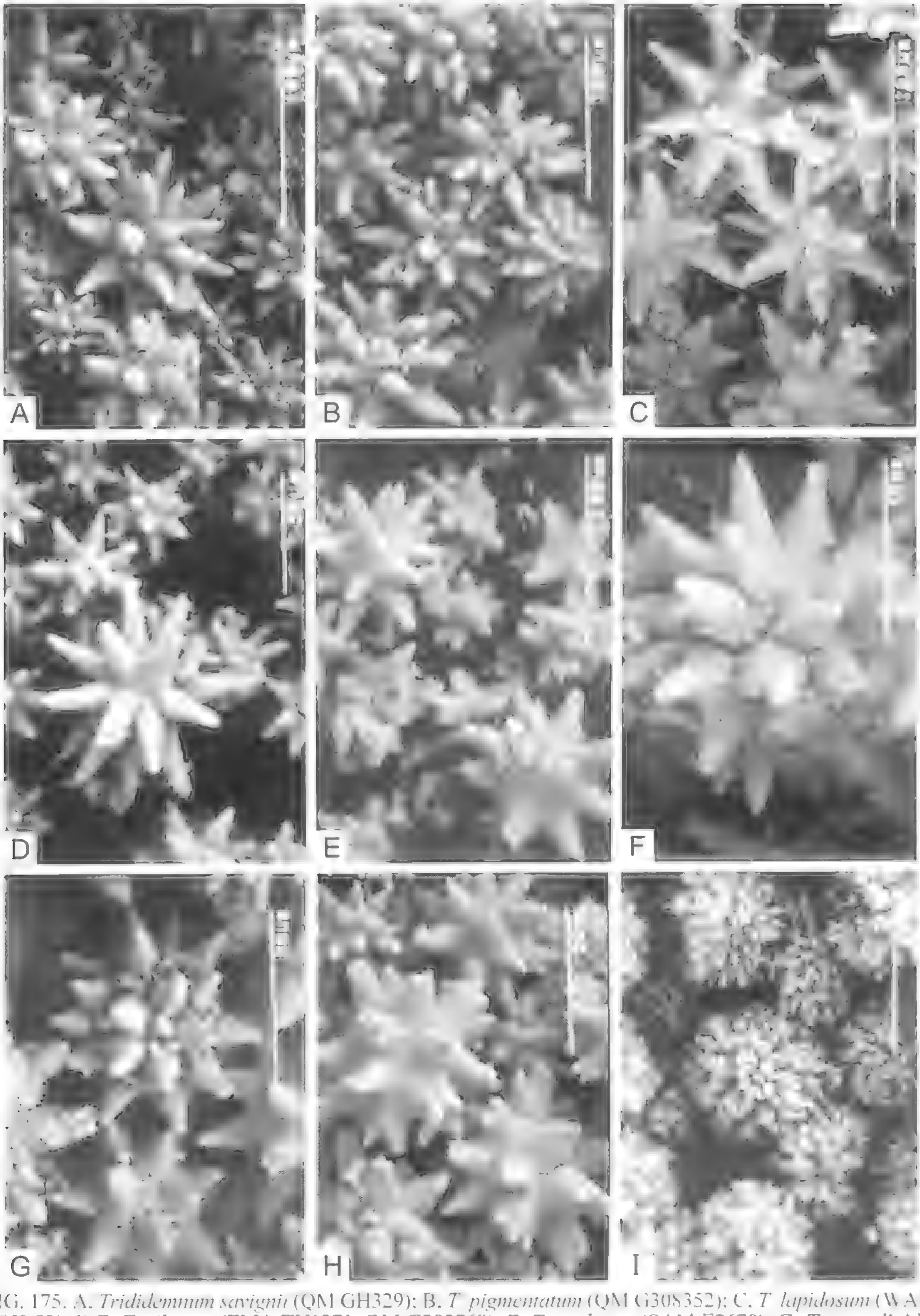


FIG. 175. A. *Trididemnum savignii* (QM GH329); B. *T. pigmentatum* (QM G308352); C, *T. lapidosum* (WAM 768.88); D,E, *T. sibogae* (ZMA TU1271, QM G303768); F, *T. caelatum* (SAM E2670); G, *T. paraclinides* (WAM617.89); H, *T. cristatum* (AM Y2321). I, *Lissoclinum punctatum* (QM GH5290).

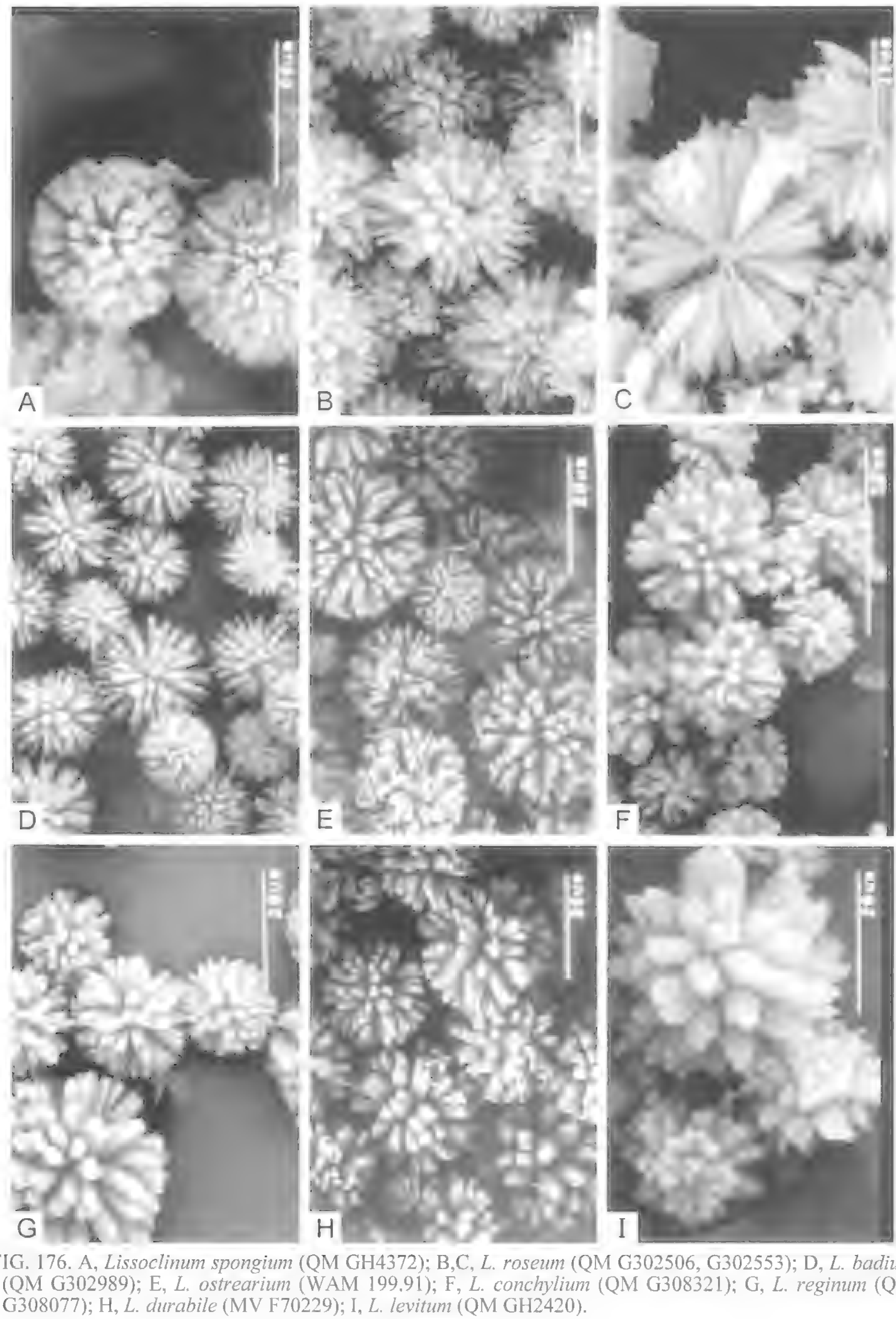


FIG. 176. A, *Lissoclinum spongium* (QM GH4372); B,C, *L. roseum* (QM G302506, G302553); D, *L. badium* (QM G302989); E, *L. ostrearium* (WAM 199.91); F, *L. conchylium* (QM G308321); G, *L. reginum* (QM G308077); H, *L. durabile* (MV F70229); I, *L. levitum* (QM GH2420).

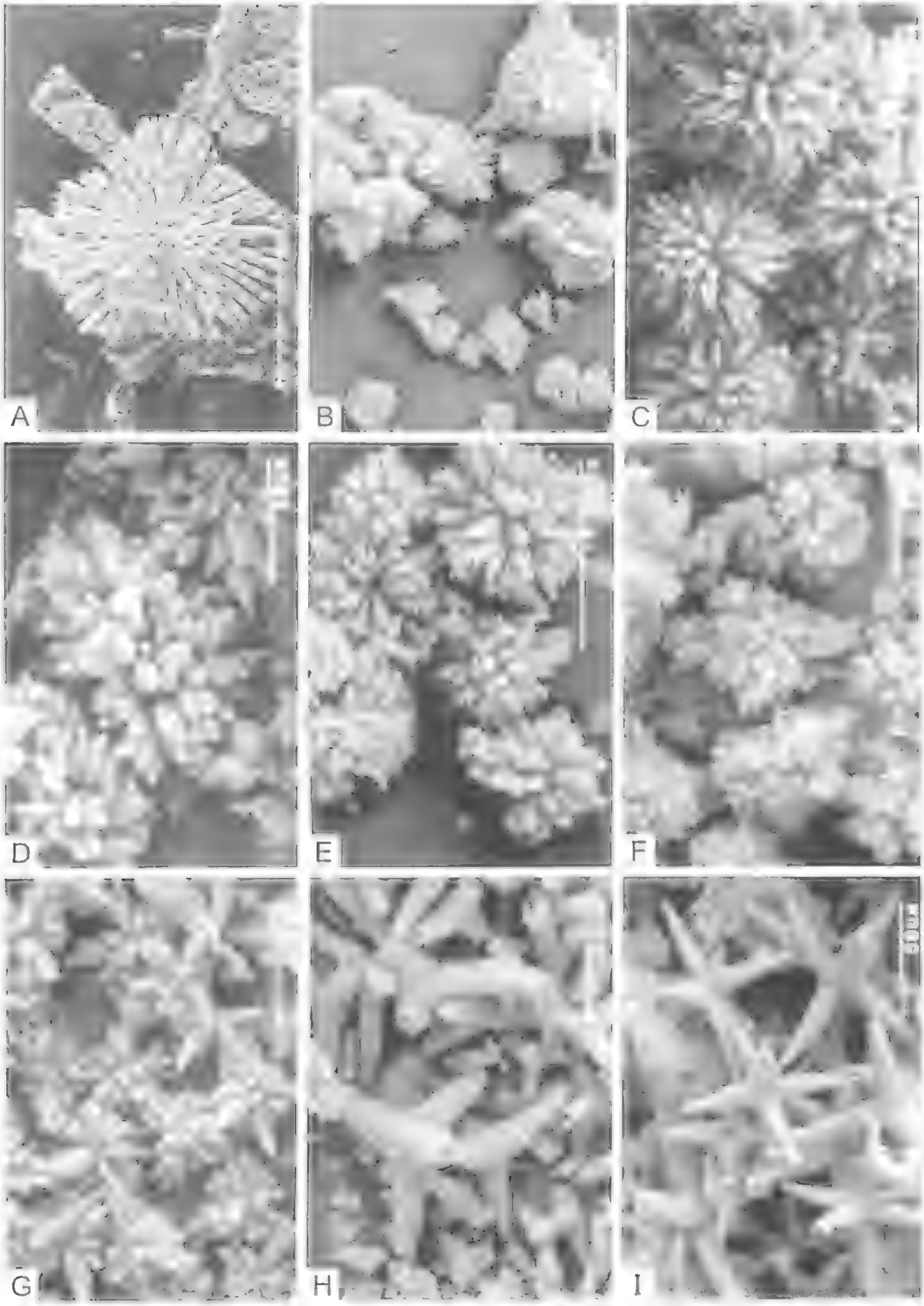


FIG. 177. A, *Lissoclinum triangulum* (QM G12623 – scale 0.05mm); B, *L. calycis* (QM G308339); C, *L. caliginosum* (QM G308271); D, *L. maculatum* (QM G302236); E, *L. nebulosum* (QM G301576); F, *L. limosum* (QM G302330); G, *L. taratara* (QM GH335); H, *L. sente* (QM GH59); I, *L. tasmanense* (QM GH1288).

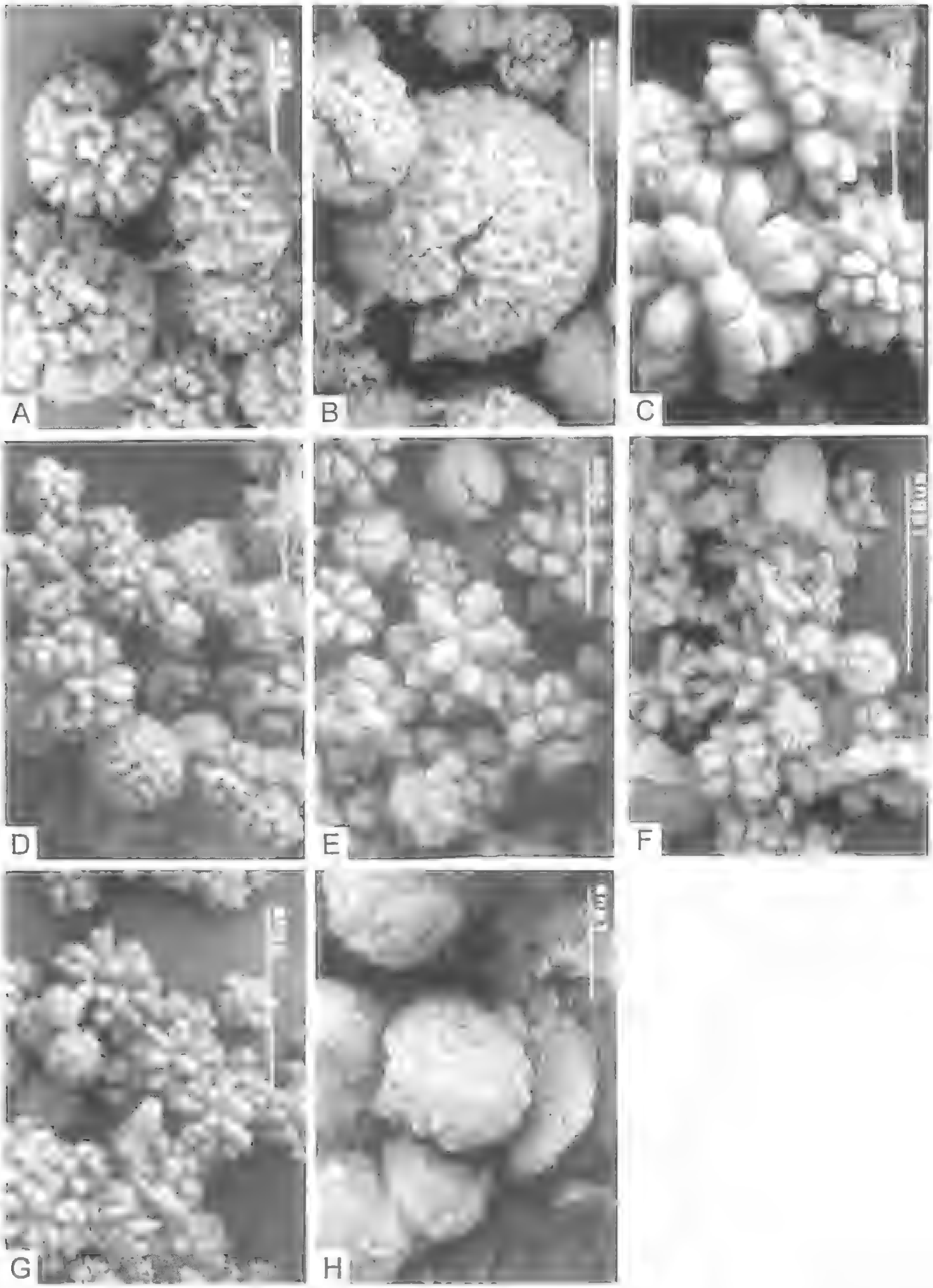


FIG. 178. A, *Lissoclinum bistratum* (QM G308659); B, *L. patella* (QM G305714); C-E, *L. timorense* (ZMA TU1274 – C,D; QM GH158 – E); F, *L. variabile* (QM G308008); G, *L. concavum* (SAM E2691); H, *Diplosoma ferrugeum*, morula bodies in the test.

PLATE 1. A, *Atriolum bucinum* (Houtman's Abrolhos W.A., QM G304670); B, *A. lilium* (Flinders I. S.A., QM GH2385); C, *A. marinense* (Marion Reef Coral Sea, QM G301616); D, *A. robustum* (Swain Reefs GBR, QM G305675); E, *A. tubiporum* (Fault Line 20m King George Sound W.A.). F, *Leptoclinides albamaculatus* (Heron I. GBR, QM G308274); G, *L. brandi* (Heron I. GBR, QM G308194); H, *L. cavernosus* (Exmouth Gulf W.A., QM G302942).

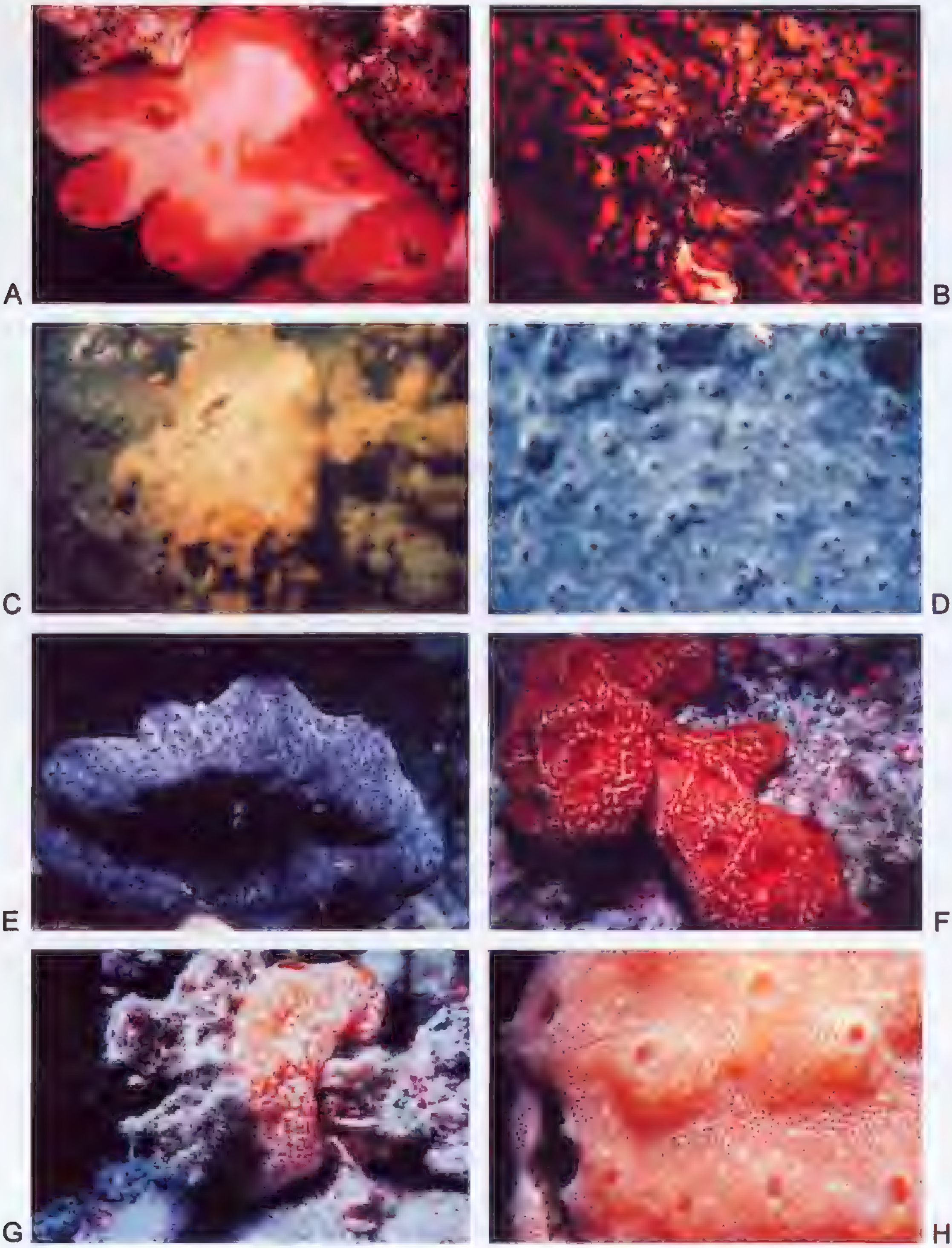
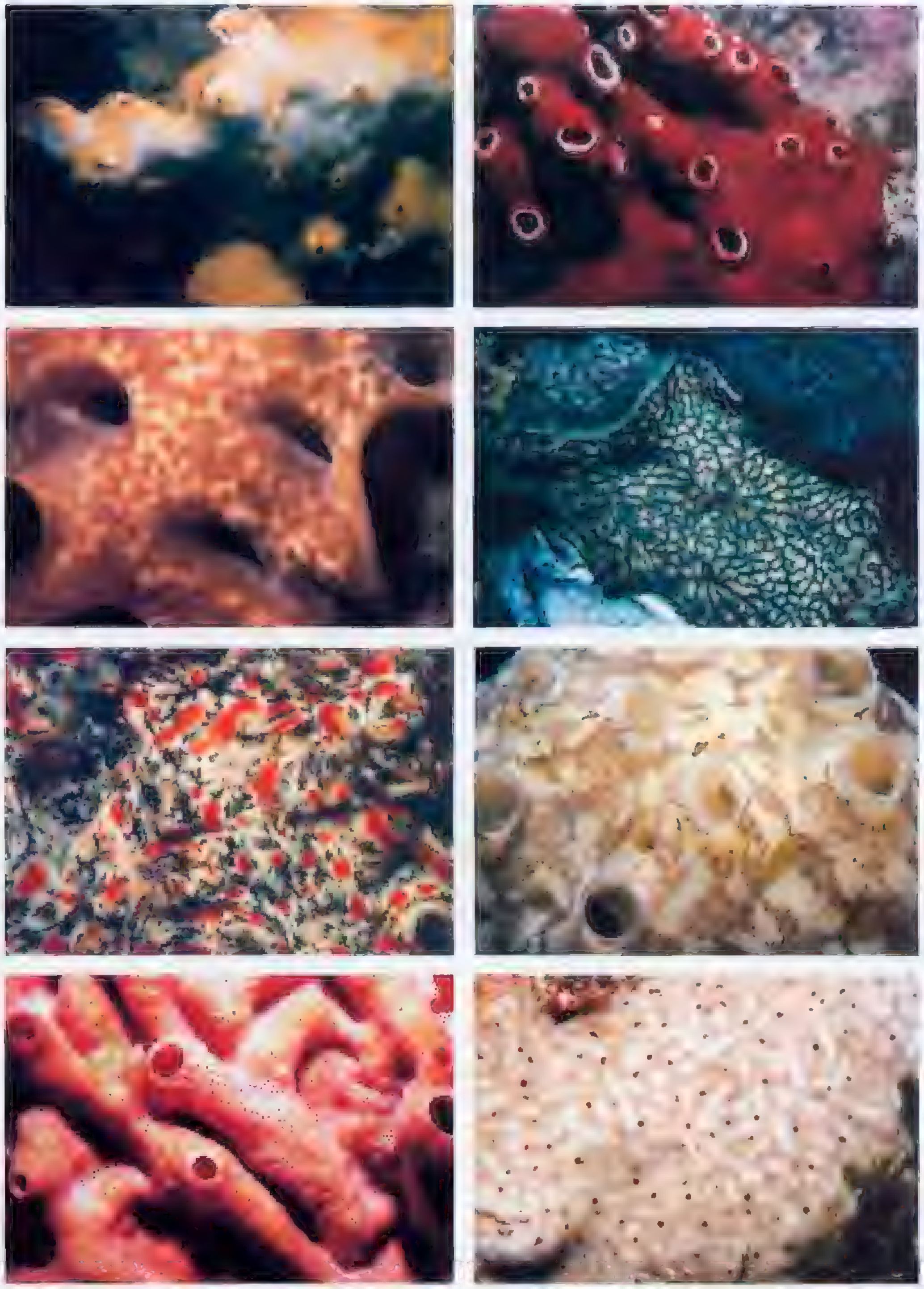


PLATE 2. A, *Leptoclinides coelenteratus* (Rottnest I. W.A.); B, *L. compactus* (Peforated I. S.A., QM G301589); C, *L. constellatus* (Haselwood I. S.A., QM G302924); D, *L. cuspidatus* (N of Barrow I. W.A., QM G300956); E-H, *L. dubius* (Swain Reefs GBR, QM G305761, G305410, G305490; Whitsunday Is Qld., QM G302936).



A B C D E F G H

PLATE 3. A,B, *Leptoclinides durus* (Whitsunday Is GBR, QM G302947; Bonaparte Archipelago, QM G302888); C, *L. echinus* (Dampier Archipelago, QM G302871); D, *L.exiguus* (Point Turton S.A., SAM E2624); E, *L. imperfectus* (Albany W.A., QM G302883); F, *L. kingi* (Buccaneer Archipelago, QM G302870). G, *L. levitatus* (Rockingham W.A. QM G5456); H, *L. maculatus* (Tipara Reef S.A., QM G301572).

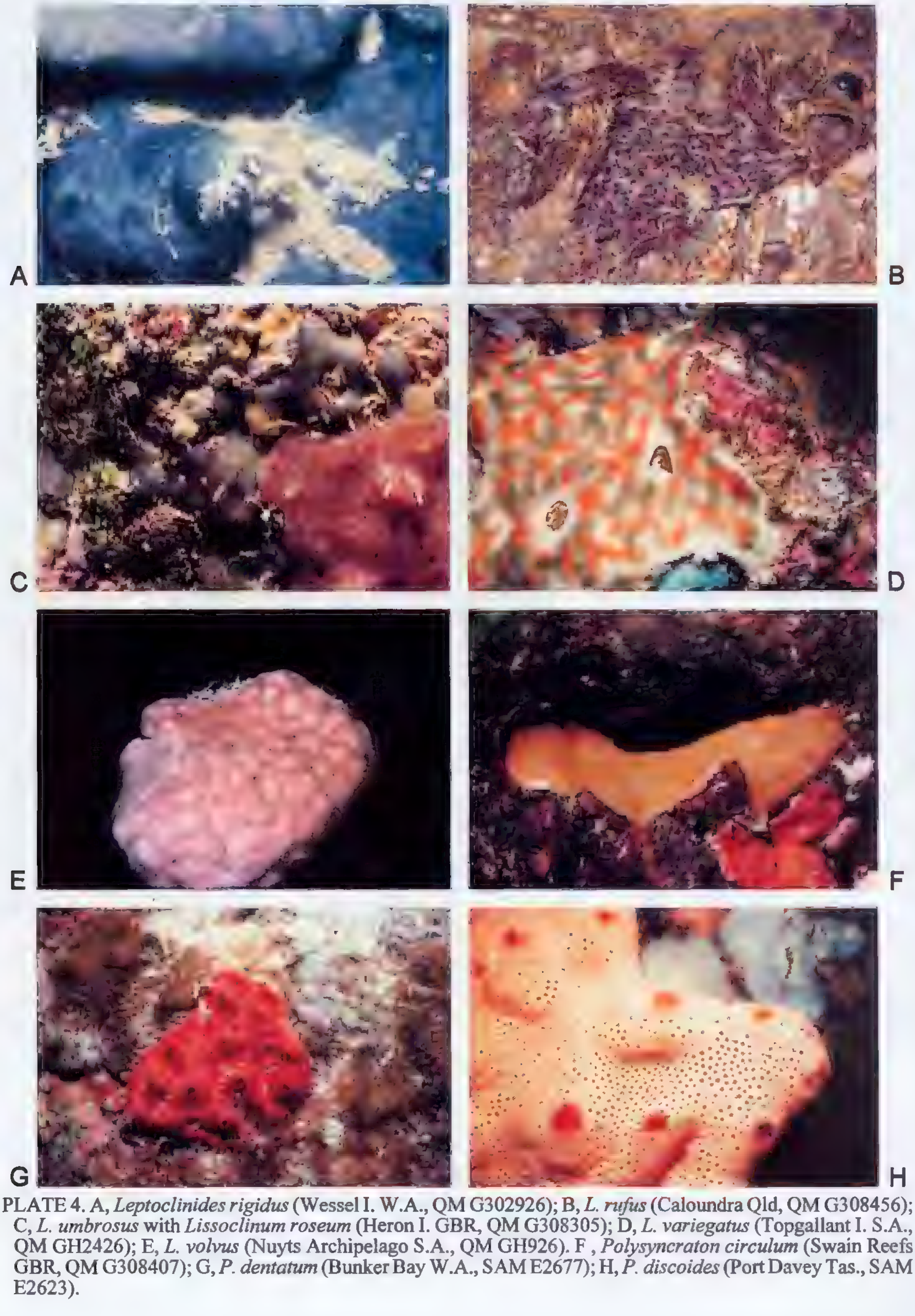


PLATE 4. A, *Leptoclinides rigidus* (Wessel I. W.A., QM G302926); B, *L. rufus* (Caloundra Qld, QM G308456); C, *L. umbrosus* with *Lissoclinum roseum* (Heron I. GBR, QM G308305); D, *L. variegatus* (Topgallant I. S.A., QM GH2426); E, *L. volvus* (Nuyts Archipelago S.A., QM GH926). F , *Polysyncraton circulum* (Swain Reefs GBR, QM G308407); G, *P. dentatum* (Bunker Bay W.A., SAM E2677); H, *P. discoides* (Port Davey Tas., SAM E2623).

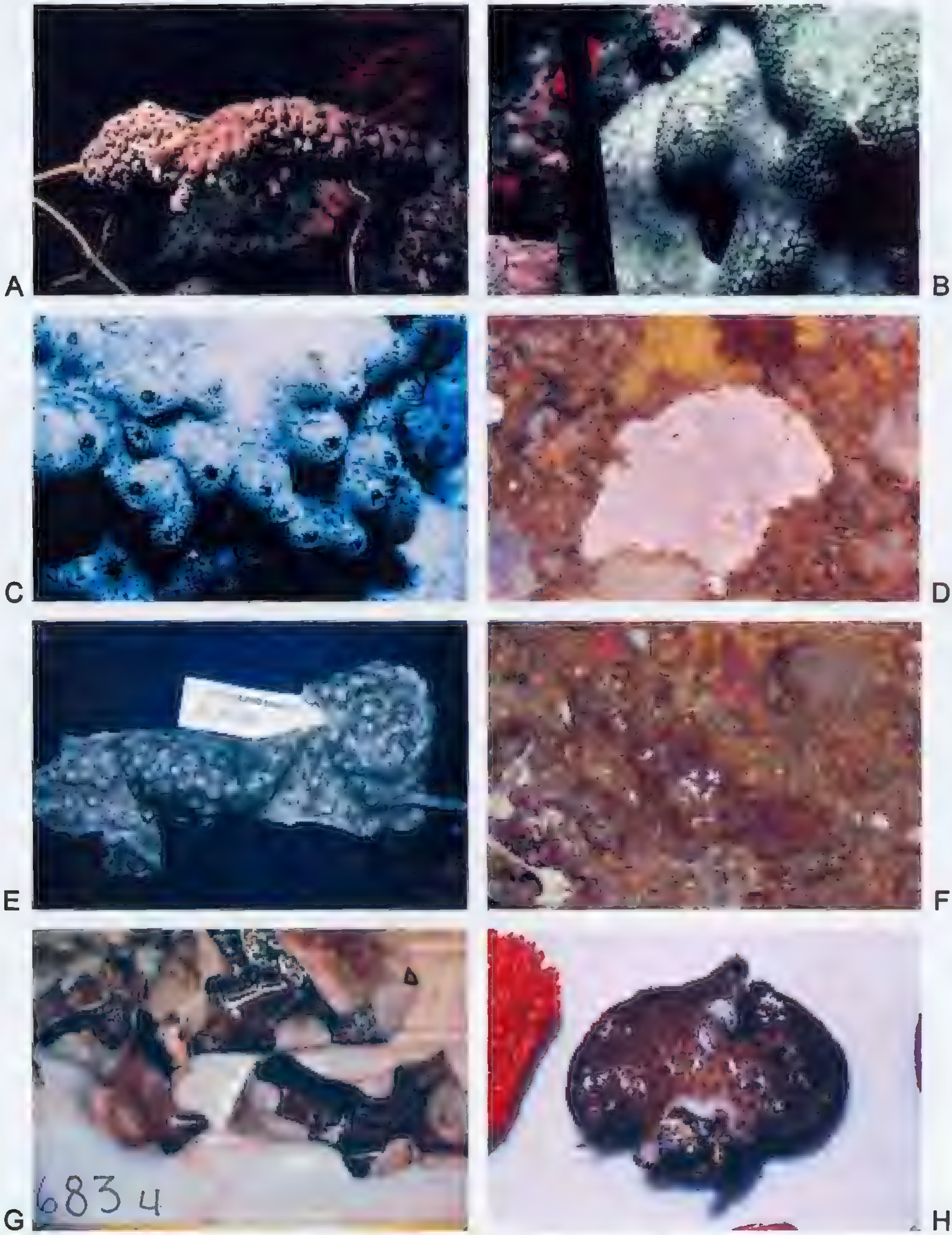


PLATE 5. A-C, *Polysyncraton echinatum* (Bowden Reef GBR, QM G300993; Whitsunday I. Qld, QM GH5370; Lizard I. GBR, QM G304176); D, *P. flammeum* (Caloundra Qld., QM G308461); E, *P. glaucum* (Swain Reefs GBR, QM G305589); F, *P. meandratum* (Caloundra Qld, QM G308460); G, *P. millepore* (Whitsunday Is Qld., QM G302945); H, *P. multiforme* (Houtman's Abrolhos W.A., QM G304641).

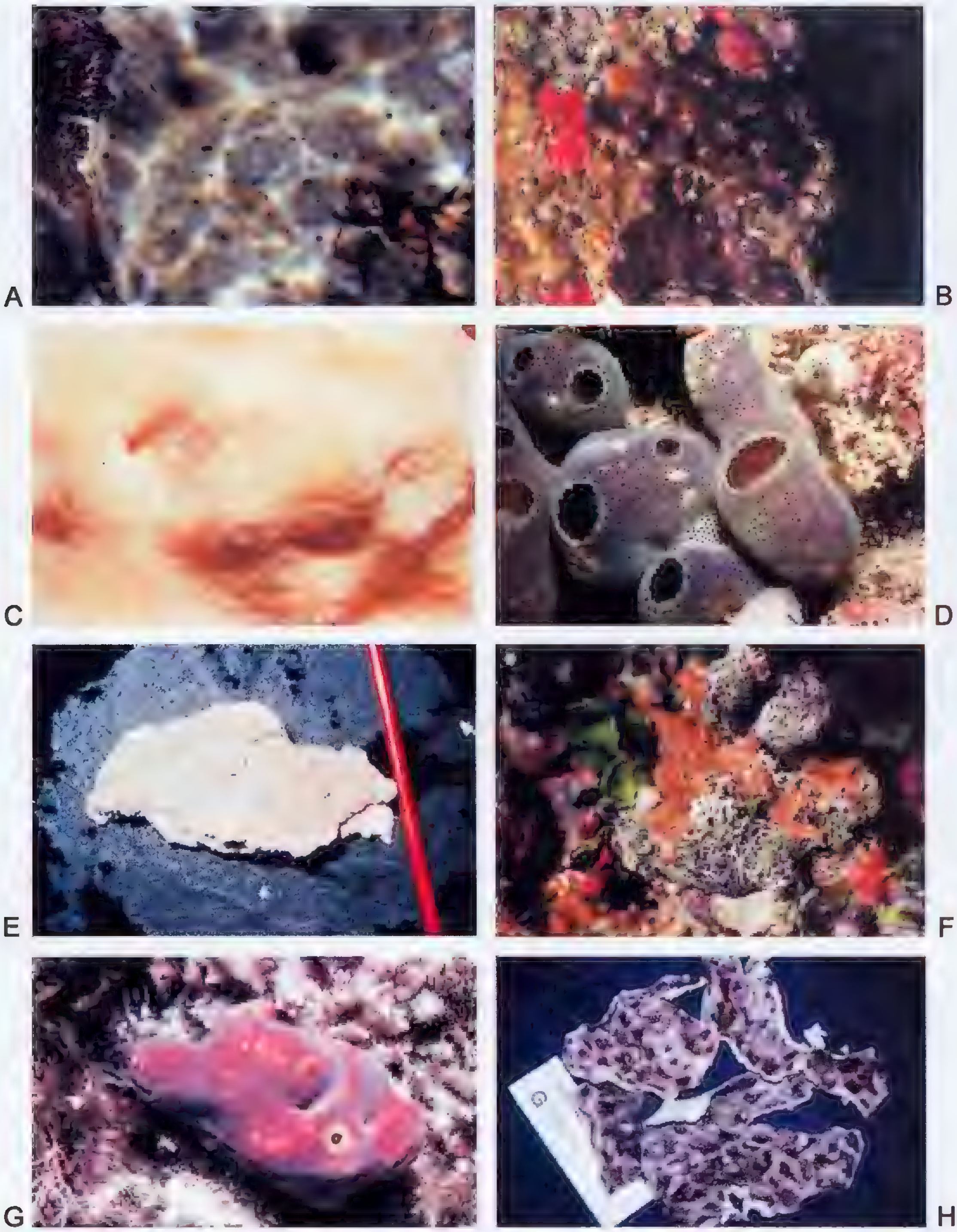


PLATE 6. A, *Polysyncraton oceanium* (Heron I. GBR, QM G308203); B, *P. oteutue* (Swain Reefs GBR, QM G308378); C, *P. palliolum* (Rottnest I. W.A., QM G300988); D, *P. pedunculatum* (Flinders I. S.A., QM GH 2387); E, *P. pseudorugosum* (Bathurst I. N.T., QM G302910); F, *P. purou* (Heron I. GBR, QM G308230); G, *P. rica* (Kangaroo I. S.A., QM GH5426); H, *P. rugosum* (Swain Reefs GBR, QM G305554).

PLATE 7. A,B, *Didemnum albopunctatum* (Whitsunday Is Qld, QM GH5367 in situ and deck shot); C,D, *D. arancium* (Swain Reefs GBR, QM G308437 G305374); E, *D. astrum* (Swain Reefs GBR, QM G305409); F,H, *D. bicolor* (Top Gallant I. S.A., QM GH2410; Ward I. S.A., QM GH2409); G, *D. chartaceum* (W. Thailand, QM GH G300950).

PLATE 8. A,B, *Didemnum candidum* (Swain Reefs GBR, QM G308391, G305557); C-E, *D. clavum* (Darwin N.T., QM G300930; Buccaneer Archipelago W.A., QM G302914, G300961); F, *D. cuculliferum* (Heron I. GBR, QM G308244); G, *D. delectum* (Edithburgh S.A., SAM E2625); H, *D. elongatum* (Tydeman Reef GBR, QM G302906).

PLATE 9. A, *Didemnum fragile* (Swain Reefs GBR, QM G308366); B, *D. fragum* (Point Souttar S.A., QM GH5438); C, D, *D. fucatum* (Deloraine I. Qld, QM GH5753); E,F, *D. granulatum* (Hardy Reef GBR, QM G300923; Black Reef GBR, QM GH5379); G, *D. grande* (Whitsunday Is, QM GH5365); H, *D. guttatum* (Swain Reefs GBR, QM G305451).

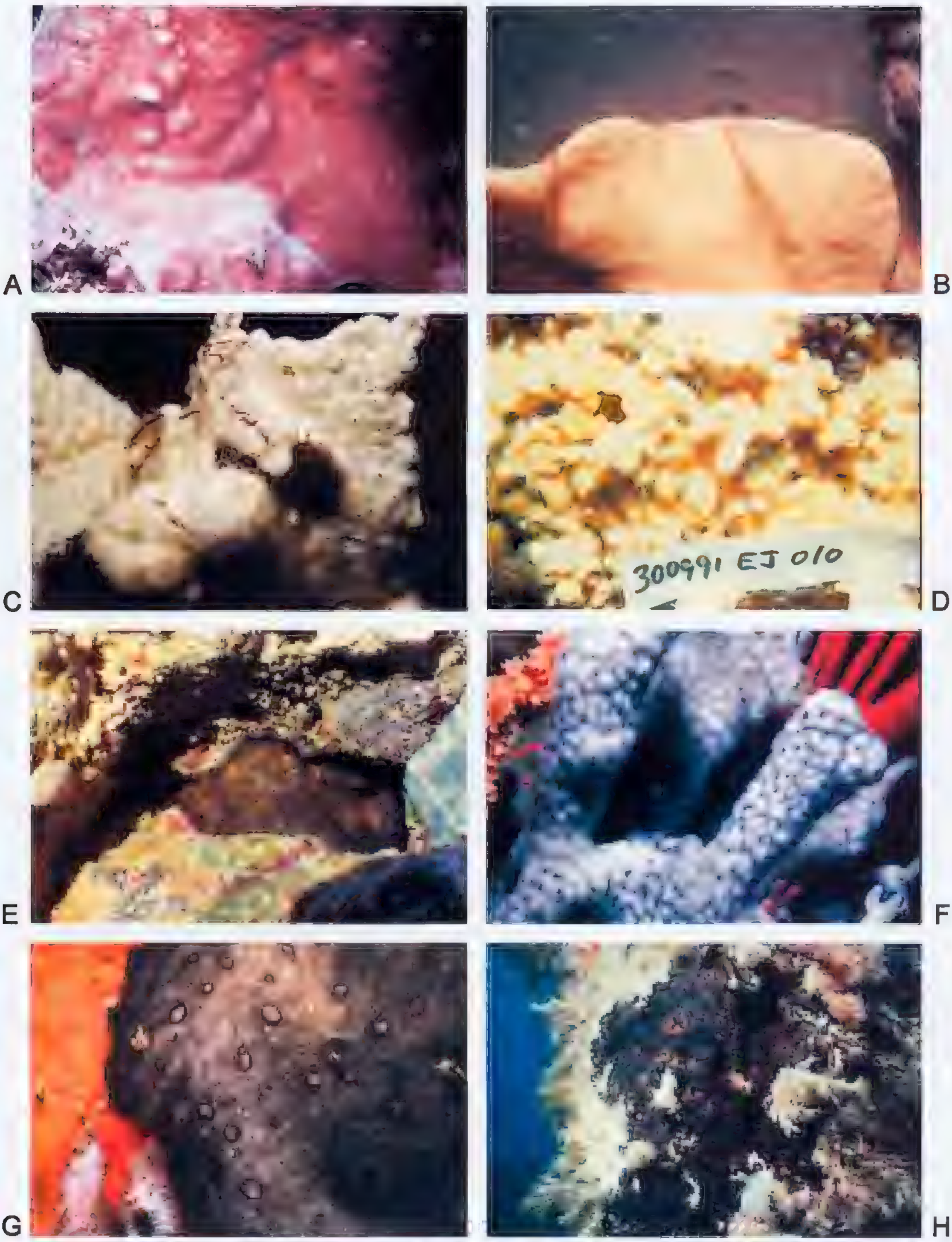


PLATE 10. A, *Didemnum herba* (Big Broadhurst Reef GBR, QM G308641); B, *D. inveteratum* (Lord Mayor Shoal W.A., QM G302922); C,D, *D. incanum* (Shell Harbour N.S.W., QM G304557; St Vincent Gulf S.A., QM G302766); E,F, *D. jedanense* (Heron I., GBR, QM G308294 – with few spicules; Cape Ruthiers W.A., QM G300976); G,H, *D. jucundum* (Esperance W.A., SAM E2693; Kangaroo I. S.A., QM G302897).

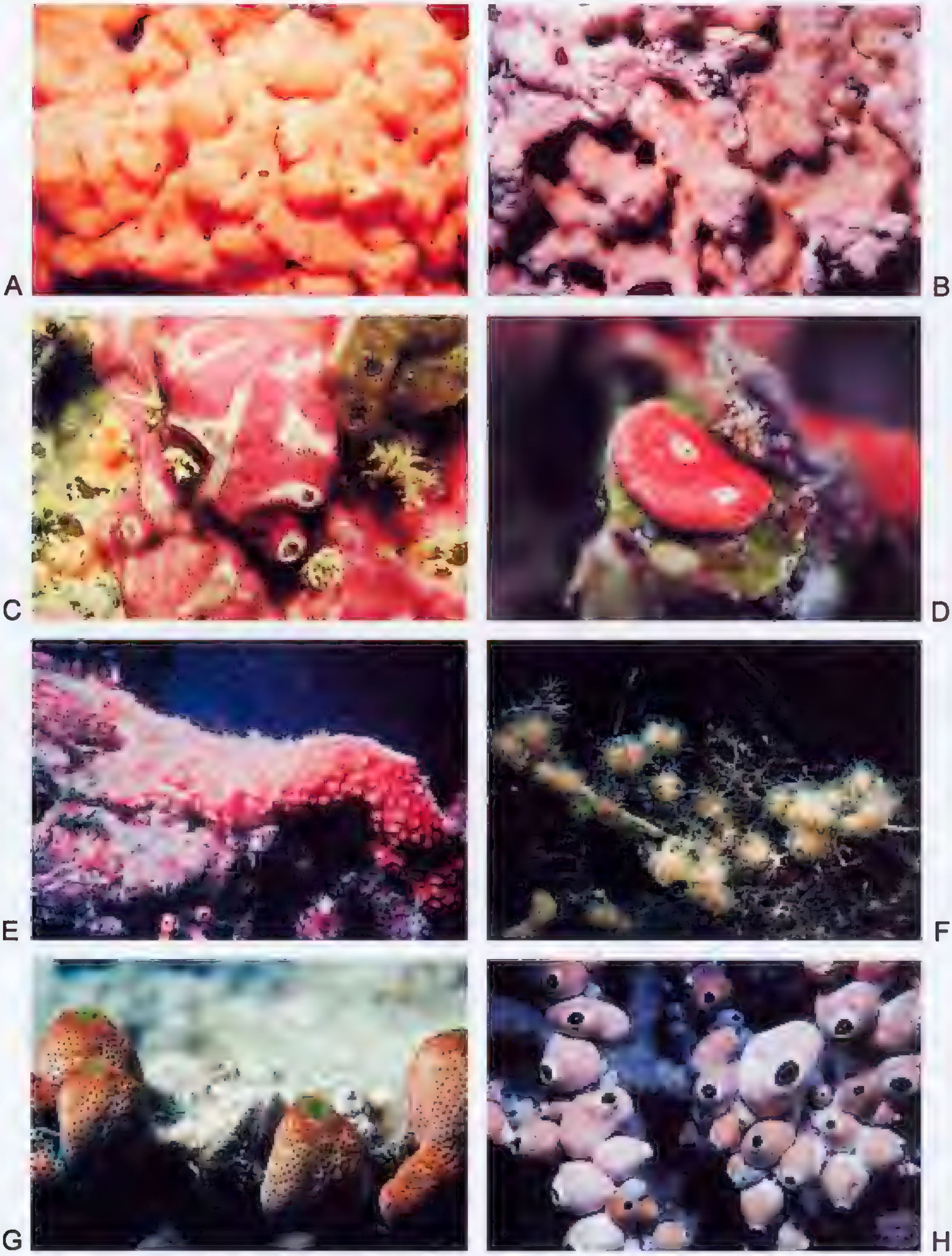


PLATE 11. A,B, *Didemnum lissoclinum* (Jervis Bay N.S.W., QM G302879; Kangaroo I. S.A., QM G300981); C-E, *Didemnum membranaceum* (Heron I., GBR, AMPI 148, G308255; Swain Reefs GBR. 305558); F, *D. minisculum* (Stansbury Jetty S.A., SAM E2647); G,H, *D. molle* (Bowden Reef GBR, QM G302921; Swain Reefs GBR, QM G305708).

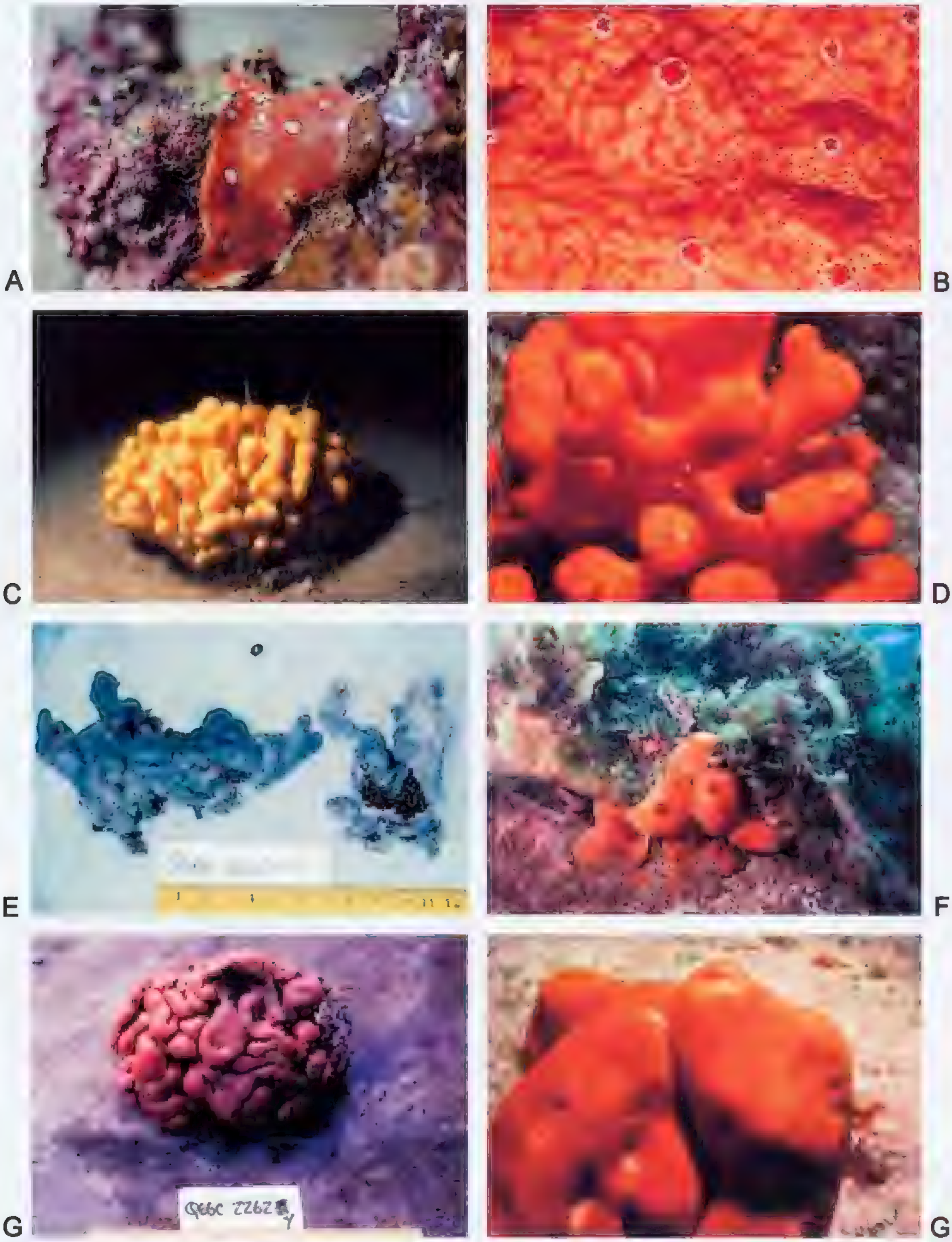


PLATE 12. A,B, *Didemnum multispirale* (Capricorn Group GBR, QM G308313; AMPI 90); C,D, *D. ossium* (English Company I. N.T., QM G302908; Lord Mayor Shoal W.A., QM G300967); E, *D. patulum* (Western Port Vict., QM G302899); F-H, *D. pecten* (Pt. Souttar S.A., QM GH 5439; Kangaroo I. S.A., G300929; Jervis Bay N.S.W., QM G302898).

PLATE 13. A-C, *Didemnum pellucidum* (Rottnest I. W.A., QM G300985; Yallingup W.A., SAM E2696; Port Giles S.A., QM G300944); D-F, *D. perplexum* (Swain Reefs GBR, QM G305796-7 G305622); G, *D. poecilomorpha* (Gazelle Peninsula PNG, QM G302890); H, *D. precocinum* (Swain Reefs GBR, QM G308368).

PLATE 14. A-D, *Didemnum psammatode* (Yorke Peninsula S.A., A,B, QM G300972; C, SAM E2611; D, Cape Wilberforce N.T., QM G302903); E-H, *D. roberti* (Bonaparte Archipelago W.A., QM G302932; Bathurst I. N.T., QM G302907; Montebello Is W.A., QM G302937; Hut Point W.A., QM G300924).

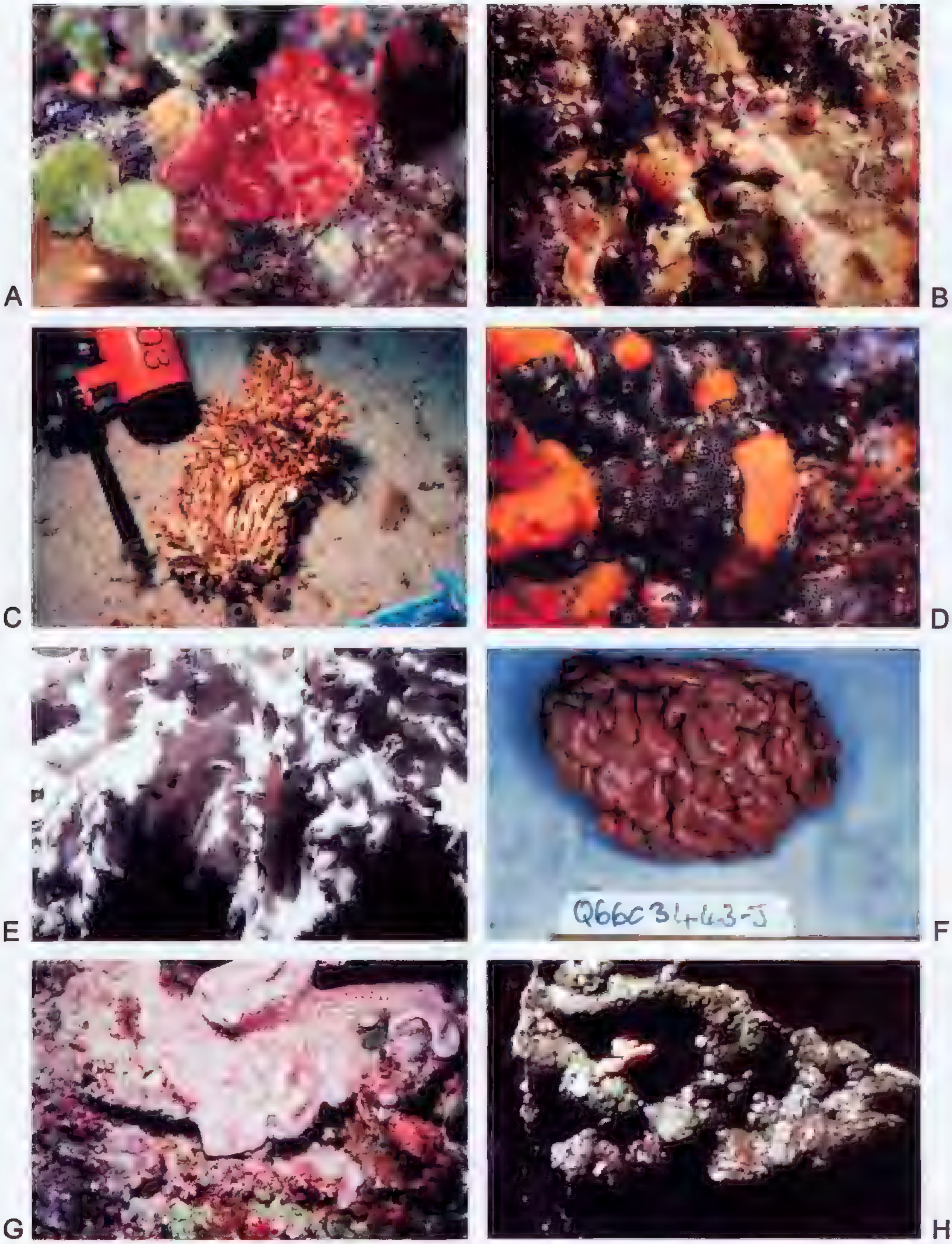


PLATE 15. A, *Didemnum scopi* Heron I. GBR, QM G308213); B, C, *D. sordidum* (Heron I. GBR, QM G308303; Lord Mayor Shoal W.A., QM G300932); D, *D. spadix* (Busselton W.A., SAM E2686); E, *D. spongioide* (Hawkesbury I. Qld, QM GH5343); F, *D. sucosum* (Western Port Vict., QM G300980); G, *D. vahatuio* (Swain Reefs GBR, QM G305373); H, *D. verdantum* (Bathurst I. N.T., QM GH5358).

PLATE 16. A, *Trididemnum areolatum* (Swain Reefs, QM G308426); B, *T. discrepans* (Phuket Thailand, QM G300938); C,D, *T. lapidosum* (Surrier I. W.A., QM G308687 G300983); E,F, *T. nobile* (Ceduna S.A., SAM E2630 E2633); G, *T. nubilum*(Heron I. GBR, QM G308443); H, *T. pigmentatum* (Heron I. GBR, QM G308316).

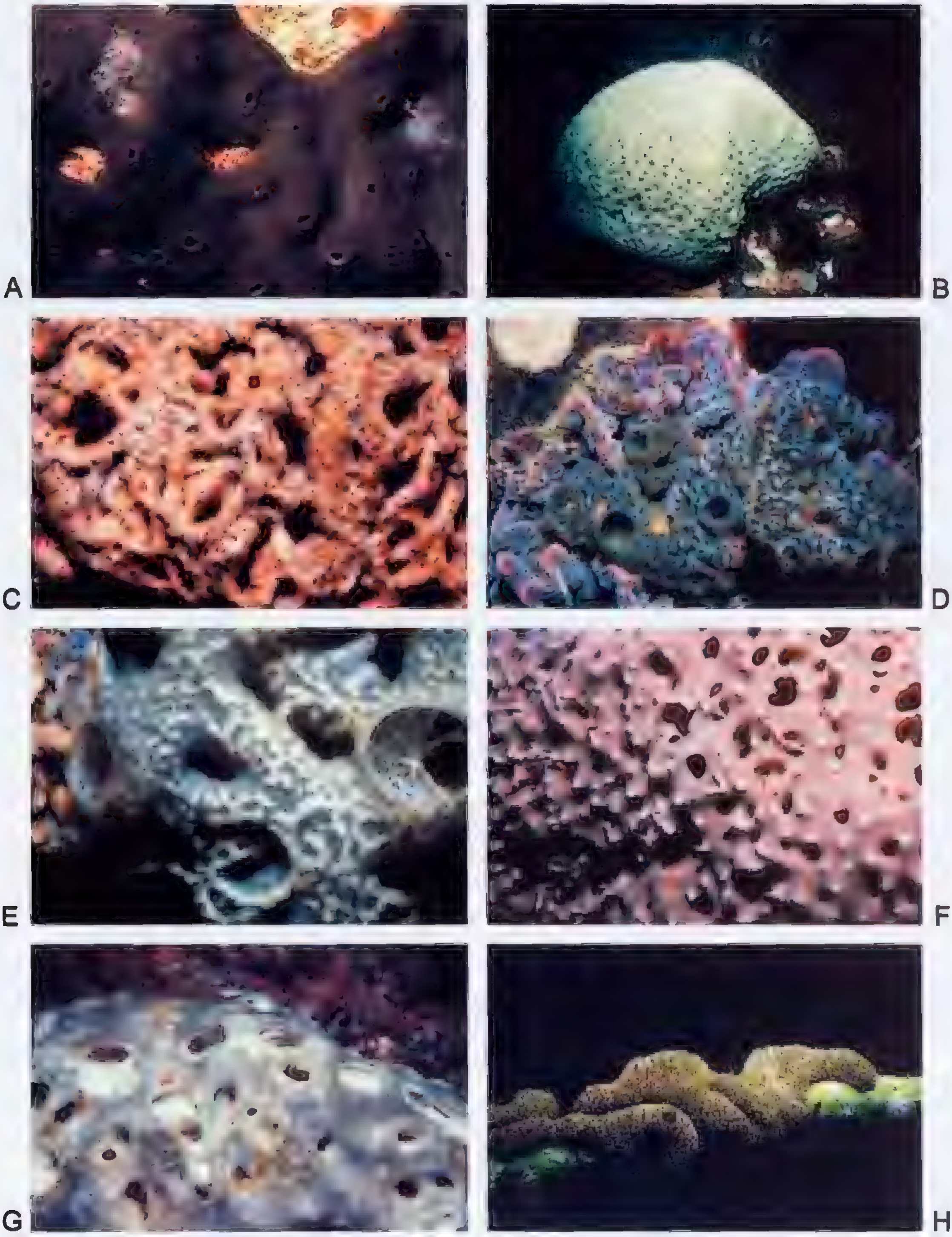


PLATE 17. A, *Trididemnum savignii* (Nares Rock W.A., QM G300965); B-G, *T. sibogae* (Western Port Vict., QM G300971; Point Turton S.A., QM G300935, SAM E2605; Port Victoria S.A., SAM E2847; Kingston S.A., QM G302875; Arrawarra N.S.W., QM G302891); H, *T. spumosum* (Edithburgh S.A., SAM E2616).

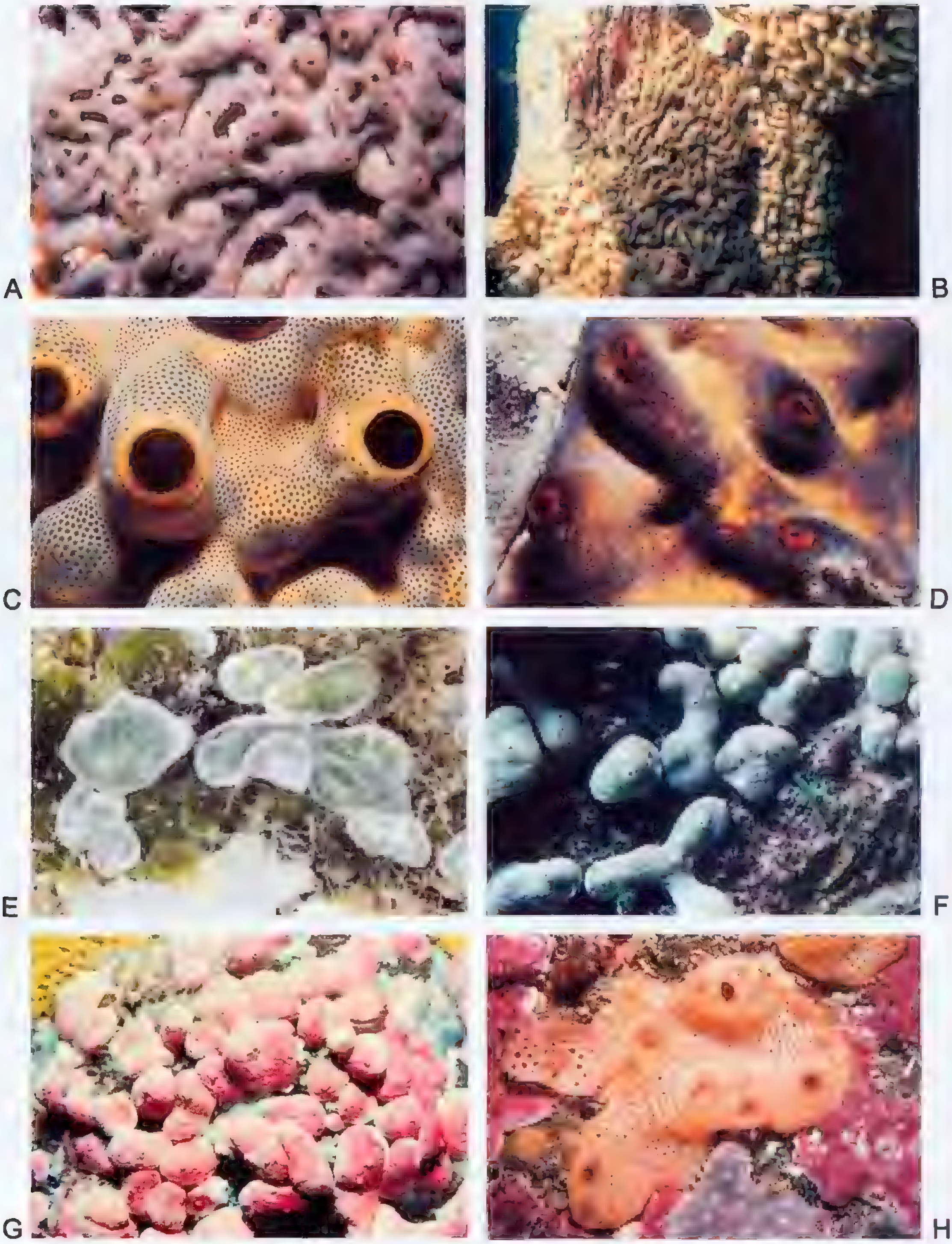


PLATE 18. A,B, *T. vermiforme* (Beachport S.A., QM G300960); C,D, *Lissoclinum badium* (Heron I. AMPI 206, 198); E-G, *L. bistratum* (Heron I. GBR; Big Broadhurst Reef GBR, QM G300978; Marion Reef AMPI 204, QM G10170); H, *L. concavum* (Flinders I. S.A., QM G308447).

PLATE 19. A, *L. Lissoclinum conchylium* (Moreton Bay Qld, QM G308499); B, *L. durabile* (Esperance W.A., SAM E2848); C, *L. levitum* (Ward I. S.A., QM GH2420); D, *L. limosum* (Swain Reefs GBR, QMG308419); E,F,. *L. nebulosum* (Whitsunday Is Qld., QM G302923); G,H, *L. patella* (Bowden Reef GBR, QM G300974; Madang PNG).

PLATE 20. A-D, *Lissoclinum reginum* (Swain Reefs GBR, QM G305456, G305800; Heron I. GBR, QM G308300 G308302); E,F, *L. roseum* (Heron I. GBR, QM G308309, G308311) see also Pl.4C; G,H, *Lissoclinun tasmanense* (King George Sound W.A., SAM E2688; Point Norton S.A., SAM E2621).

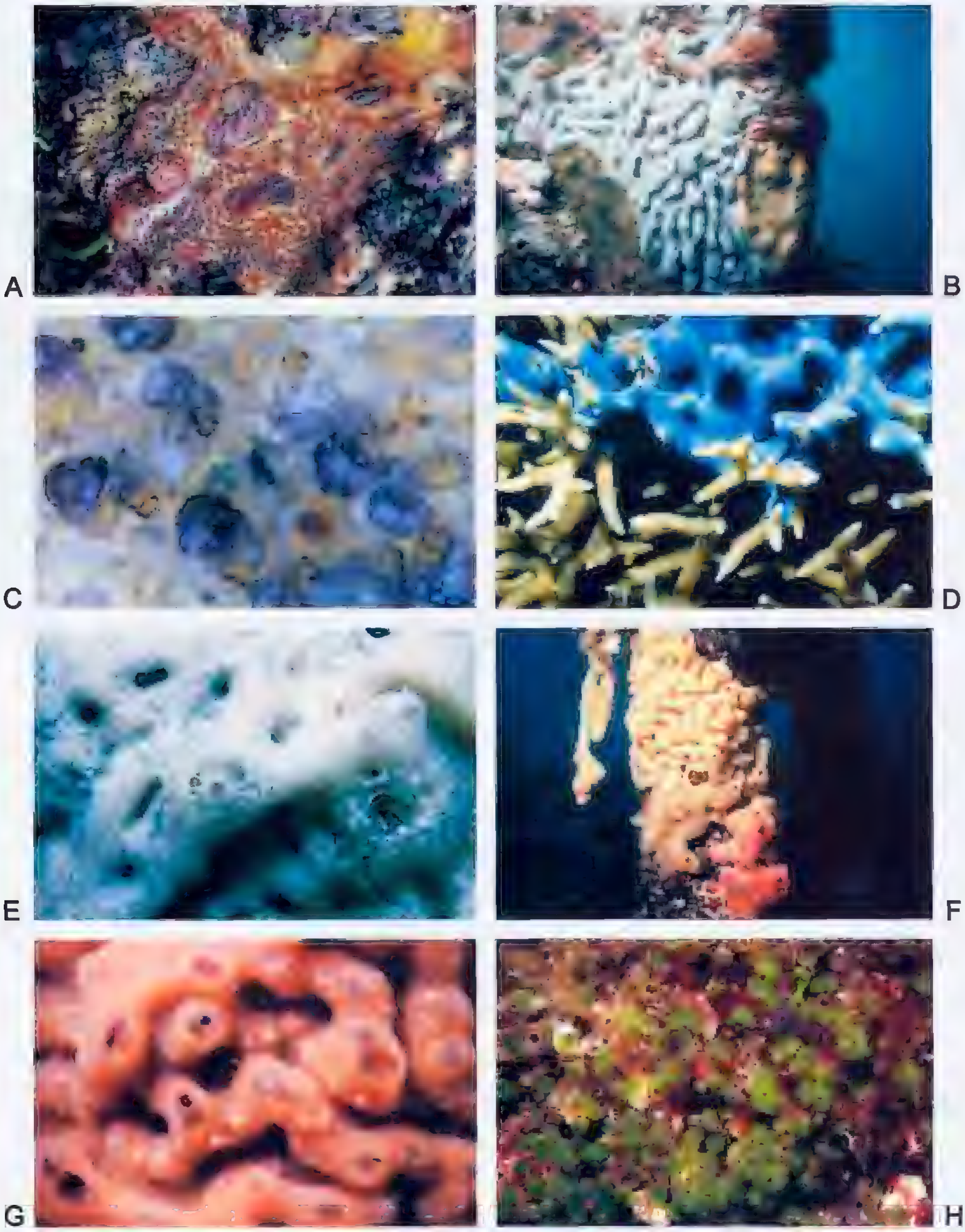


PLATE 21. A, *Diplosoma ferrugeum* (Heron I. GBR, QM G302952); B, C, *D. listerianum* (Beachport jetty S.A., QM G302880; Sydney Harbour, on sandstone blocks); D, *D. simile* (Rabaul PNG); E, *D. translucidum* (Cape Ruthiers W.A., QM G302946); F,G, *D. velatum* (Kangaroo I. S.A., QM G302911); H, *D. virens*, small colonies (Moreton Bay Qld).

COLOUR PLATES, ACKNOWLEDGMENTS

Aims Bioactivity Group, 1H; 2C,D,H; 3A-C,E-G; 4A; 5A,B,G; 6C,E,G; 7A,B,G; 8C-E,H; 9B-H;10A,B,F,H; 11A,B,G; 12C-H; 13A,F; 14A,B,D-H; 15E,F,H; 16B-D; 17A-C,F-G; 18A,B,F; 19E-G; 21B,E-G

Clay Brice, West Australian Museum, 1A, 5H

Alan Butler, University of Adelaide, 10D

Neville Coleman, 1C,E; 11C; 12B; 16G; 18C,D,G; 19A; 21H

Tim Glasby, 21C

Karen Gowlett Holmes, 3D; 4 G,H; 8G; 10G; 11F; 13B; 14C; 15D; 16E,F; 17D,E,H; 19B; 20G,H

Nigel Holmes, 1B; 2A; 4D,E; 6D; 7F,G; 18H; 19C

Susan List, Queensland Museum, 1D; 2E-G; 4F; 5C,E; 6B,H; 7C-E; 8A,B; 9A; 11E,H; 13C-E,G; 15A,G; 16A; 19D; 20A,B

L. Miller, Water Board of Sydney, 10C

Myriam Preker, Heron I. Research Station, 1F,G; 4C; 6A,F; 8F; 10E; 11D; 12A; 13H; 15B,C; 16H; 20 C-F; 21A

John Ryland, 18E

W.H. Sasse, 2B

Scoresby A. Shepherd, 3H

Roger Steene, 19H; 21D

Jeff Wright, Queensland Museum, 4B; 5D,F

INDEX TO TAXONOMIC NAMES

(pages on which formal descriptions and figures appear are shown in **bold**)

THE AUSTRALIAN ASCIDIACEA PARTS 1–3, CORRIGENDA

PATRICIA KOTT

Kott, P. 2001 08 15: The Australian Ascidiacea parts 1–3, corrigenda. *Memoirs of the Queensland Museum* **47**(1): 409-410. Brisbane. ISSN 0079-8835.

The following are corrections to typographical and other errors detected in the preceding 3 parts of the Australian Ascidiacea and its supplements (Kott 1985, 1990a,b and 1992a,b).

PART 1 PHLEBOBRANCHIA AND STOLIDOBRANCHIA (Kott, 1985)

p. 25 column 2, key couplet 1, 10 to read: 11

p. 37 column 1, line 7 in NEW RECORDS delete: GH2495

p. 39 column 2, line 6, somtimes to read: sometimes

p. 43 column 1, line 3 in NEW RECORDS, GH2518 – 22 to read: GH2518–20 GH2522

p. 61 column 1, synonymy of *Phallusia arabica* to read:
Phallusia arabica Savigny, 1816, p.164. Hartmeyer, 1915b, p.414. Michaelsen, 1919, p.113.
? *Ascidia depressiuscula* Heller, 1878, p.5. (**Not** Herdman, 1906, p.305 < *Ascidia* sp.).
Phalllusia depressiuscula : Van Name, 1918, p.116, Tokioka, 1970, p.87.
Phallusia julinea: Tokioka, 1952: 107 (part, specimen with anal lobules).
Phallusia philippinensis Millar, 1975, p.273 (part, not specimens from Singapore, see *Phallusia millari* sp. nov.).

p. 61 column 1, lines 1– 2 in PREVIOUSLY RECORDED, delete: Queensland (Northwest 1 – Kott, 1966).

p. 66 column 2, line 4 in synonymy, *philippensis* to read: *philippinensis*; line 7, in NEW RECORDS, GH2494-69 to read: GH2494-7; last line, GH2495-9 GH2502-3 to read: GH2498-9 GH2503

p. 76 column 1, line 1 in synonymy, 1900, p.76 to read: 1900, p.6

p. 80 column 1, line 2 in PREVIOUSLY RECORDED to read: holotype AM U3952, paratypes QM G4907 G4936...

p. 83 column 2, 4th last line in paragraph 3, northern-eastern to read: north-eastern

p. 85 column 1, line 6 in synonymy, *pellucidas* to read: *pellucidus*

p. 85 column 2, line 1, *Rhodosoma* to read: *Pera*

p. 86 caption Fig. 34, *Rhodosoma turcica* to read: *Rhodosoma turcicum*

p. 111 column 1, last line paragraph 3, very to read: vary

p. 112 column 2, **Styela canopus** Savigny, 1816 to read: **Styela canopus** (Savigny, 1816)

p. 112 column 2, lines 1-4 in synonymy to read:
Cynthia canopus Savigny, 1816, pp. 45,154.
Styela canopus: Herdman, 1891, p. 581. Michaelsen, 1898, p. 367 (*f. typica*); 1919, p.66. Kott, 1957, p.144. Millar, 1975, p.304. Kott & Goodbody, 1982, p.534.

p. 122 column 2, line 12 in synonymy, after *Cnemidocarpa irma* insert: Hartmeyer, 1927: 168.

p. 141 column1, line1 last paragraph and column 2, lines 2, 7 and10 in first paragraph, *exiqua* to read: *exigua*

p. 177 column 2, in synonymy, *Styela cryptocarpa*: Sluiter to read: *Styela cryptocarpa* Sluiter

Kott, P. 2001 xx xx: The Australian Ascidiacea part 4, Aplousobranchia (3), Didemnidae. *Memoirs of the Queensland Museum* **xx**(x): 1-xxx. Brisbane. ISSN 0079-8835p. 201 column 2, branchial formulae in paragraph 2 to read: DL 0(8) 2(9) 2(8) 2(9) 2 E (WAM 794.83); E2(3) 3(6) 3(8) 2(5) 3 DL (ZMA TU976.32).

p. 210 column 2, **Monandrocarpa plana** (Kott, 1972) to read: **Monandrocarpa plana** Kott, 1972

p. 210 column 2, between lines 1 and 2 in synonymy, insert: *Cnemidocarpa incubita* Tokioka, 1967, p.186

p. 214 column 1, line 28 Herdman, 1898 to read: Herdman, 1891

p. 215 column 1, line 5 from bottom, Mand to read: and

p. 217 column 1, line 3 in NEW RECORDS and line 14 in EXTERNAL APPEARANCE, QM G9484 to read: QM GH2223

p. 217 column 2, last line paragraph 3, after specimens insert: QM G2223; line 4 from bottom, *Polycarpa* to read: *Polyandrocarpa*

p. 222 column 2, lines 7 to 9, delete: more .... interspace)

p. 226 Fig. 107 Scales, **a**, 2.5mm to read: **a**, 4.0mm

p. 231 column 1, line 3, to read: Type Species: *Stolonica socialis* Hartmeyer, 1903

p. 274 column 1, line 23, 391 to read: 381

p. 274 column 1, in NEW RECORDS, line 8, GH11929 to read: G11929; line 10, GH43–4 to read: GH44

p. 278 column 1, in NEW RECORDS line 10, G10157 to read: G10167; line 14, GH42–3 to read: GH43

p. 279 column 1, lines 3 and 5, *violaceum* to read: *violaceus*

p. 338 column 1, in *Rhabdocynthia pallida*, Sluiter 1898a to read: Sluiter 1898b

p. 342 column 1, in synonymy of *Halocynthia hispida*, *Cynthia dumosa* Stimpson, 1885b to read: *Cynthia dumosa* Stimpson, 1855b
Note: according to Kott (1998), *Halocynthia hispida* (Herdman, 1881) is a junior synonym of *Halocynthia dumosa* (Stimpson, 1855)

p. 344 column 1, **Halocynthia papillosa** (Linnaeus, 1767) to read: **Halocynthia papillosa** (Gunnerus, 1765)

p. 344 column 1, line 8 in synonymy, Michaelsen, 1918, p. 10 to read : Michaelsen 1919, p.12

p. 356 column 1, lines 1–2 in second paragraph, the type species of *M. propinquus* and *M. polymorphus* to read: the holotype of *M. propinquus* and specimen of *M. polymorphus*: Herdman, 1882

p. 363 column 1, **Hartmeyeria formosa** (Herdman, 1899) to read: **Hartmeyeria formosa** (Herdman, 1882)

p. 367 column 2, last line to read: not laterally flattened.......... *M. ficus*

p. 371 column 2, line 8 in paragraph 5, itsovary to read: its ovary

PART 2 APLOUSOBRANCHIA 1 (Kott, 1990a)

p. 26 column 2, line 10 in synonymy, Sluiter, 1904, p.3 to read: Sluiter, 1904, p.24

p. 57 column 2, line 3 in NEW RECORDS, after E1973–4 insert: E2471

p. 109 column 2, Genus **Distaplia** line 3 to read: Type species: *Distaplia magnilarva* Della Valle, 1881

p. 118 column 1, line 2 in TYPE LOCALITY, Bryon to read: Byron

p. 129 column 2, line 3 in TYPE LOCALITY, GH4179 to read: QM GH4179

p. 133 column 2, Genus **Hypsistozoa** Brewin, 1956b to read: Genus **Hypsistozoa**, Brewin, 1953

p. 167 column 2, line 5, delete: GH4187–8

p. 177 column 1, line 6 in NEW RECORDS, delete: G10010

p. 184 column 1, line 3 in NEW RECORDS, *GH2143* to read: *GH2142*

p. 193 column 1, Key couplet 14, dentritic to read: dendritic

p. 220 column 1, line 2 in NEW RECORDS, delete: G11941

p. 231 column 1 line 4 in TYPE LOCALITY G11942–4 to read: G11942–3

p. Pl. 13a, GH4188 to read: GH4308

PART 3 APLOUSOBRANCHIA 2 (Kott, 1992a)

p. 450 column 1, line 3 in NEW RECORDS, E2531 to read: E2550

p. 463 column 1, line 6 in synonymy, *Polyclinum pute*: Monniot to read: *Polyclinum pute* Monniot

p. 475 column 1, line 15 from bottom, 13 to read: 12

p. 490 column 2, **Synoicum galei** sp. nov. to read: **Synoicum galei** Michaelsen, 1930

p. 498 column 1, in synonymy, *Psammaplidium prunum* Herdman, 1899, p.84 to read: *Polyclinum prunum* Herdman, 1899, p.83

p. 511 column 2, last line, ...26 to read: 28

p. 567 column 1, lines 3–5 in DISTRIBUTION, delete: South Australia......SAM E2594)

p. 567 column 2, line 6 in PREVIOUSLY RECORDED, Phillipines to read: Philippines

p. 569 column 1, second last line in second paragraph, betwen to read: between

p. 570 column 2, line 5 in NEW RECORDS, SAM E2540 E2571 E2587 to read: SAM E2540 (also registered as E2587) E2571

p. 574 column 2, last line in TYPE LOCALITY, E10648 to read: E2648

p. 595 Pl.1b, has been cropped at the wrong end, and only the ends of 3 lamellae of the colony of *Condominium areolatum* remain in the top left corner.

p. 620 *Tylobranchia* to read: *Tylobranchion*

SUPPLEMENT 2 (Kott, 1992b)

All odd pages 623—655, running heading The Australian Ascidiacea 2. Supplement to read: The Australian Ascidiacea Supplement 2.

p. 625 column 1, line 2 in DISTRIBUTION, delete: E2471

p. 628 column 1, lines 4–5 in TYPE LOCALITY, delete: paratype SAM E2422

p. 635 column 1, line 3 in synonymy, 1987a, p.3 to read: 1987a, p. 28

p. 635 column 2, line 3 in synonymy, 1987a, p.5 to read: 1987a, p.25

p. 648 column 1, last line in paragraph 4, objective to read: subjective

p. 649 column 1, line 17 in synonymy, Moniot 1991 to read: Monniot, 1990; line 4 in DESCRIPTION, paricles to read: particles

p. 650 column 1, line 3 in synonymy, 1905a, p.135 to read: 1905a, p.326

p. 652 column 1, last line in paragraph 8, 205–239 to read: 239–289

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